

HABITAT FRAGMENTATION, STRIPED SKUNKS,
AND WATERFOWL NEST PREDATION

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ABSTRACT

In North America, expansion of agriculture has resulted in the fragmentation of grasslands. Consequently, waterfowl populations have declined due to predation on nests. Predation on nests is an old evolutionary force affecting waterfowl, but the recent fragmentation of grasslands may have yielded a situation to which waterfowl are not yet adapted.

In southcentral Saskatchewan, striped skunks are a major predator, and the interactions between fragmentation, striped skunks, and waterfowl are unknown, and were the major goal of my thesis. First, I examined the patterns of den site selection in striped skunks. Farmsteads are the most preferred habitat for den sites, and that within farmsteads, striped skunks denned under buildings. Alternatively, resting sites were preferably located in farmsteads and wetlands, whereas managed nesting areas, woodland, and cropland were avoided.

When foraging within their home ranges, striped skunks preferred habitats such as wetland and woodland where their main food items, insects and small mammals, are most abundant. Cropland contained little food, and was strongly avoided. Use of specific habitats decreased with distance from the habitat edge, suggesting that large patches of nesting habitat may provide a refuge for ground nesting birds.

Lastly, I performed a field experiment to assess the effects of nest density and nearest neighbours on nest predation. Density effects did not occur during the early breeding seasons of waterfowl (May 15 - June 13), even across a 10-fold difference in nest density (2.5-25 nests/ha). However, density effects were significant in the late breeding season (June 15 - July 14). Nearest neighbour effects were present at intermediate and high densities, but rarely observed at low density. Also, nearest neighbour effects occurred faster during the late breeding season, suggesting that striped skunks recognized and keyed on high-density nesting patches. This confirms that at current nest density (typically <2.5 nests/ha), density dependent predation is not a major factor affecting waterfowl. Instead, changes to the predator community, distance to predator dens, and availability of profitable foraging habitats for predators may have a stronger influence on the fate of waterfowl nests in fragmented landscapes.

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1. GENERAL INTRODUCTION

1.1 Habitat fragmentation and the creation of heterogenous landscapes

With increasing human populations and rising demands for food and space, natural habitats are constantly being converted into urban or agricultural areas (e.g., Boren et al. 1997). Remaining natural habitats are often broken into smaller patches, and isolated within vast areas of human-modified land. This process, called habitat fragmentation, has been the center of numerous studies in biology and landscape ecology (MacArthur and Pianka 1966; MacArthur and Wilson 1963, 1967; Brown 1971; Hooper 1971; Diamond 1974, 1975; Forman and Godron 1986; Lovejoy et al. 1986; Wilcove et al. 1986; Laurance and Yensen 1991).

The effects of habitat fragmentation are numerous, but can be summarized by two major alterations of the landscape: 1) reduction of the overall availability of natural areas, and/or 2) reduction of the size, but increase in the number of remaining patches (Forman and Godron 1981). Fragmented landscapes become more heterogeneous as different habitats become interspersed in a mosaic of various patches (Pickett and Cadenasso 1995).

Fragmented habitats also have more edge per unit area. Habitat edges, defined as the interface between two different habitat types (Gosz 1991), often influence the

distribution and abundance of animals (Baltz et al. 1993; Berg and Pärt 1994; LaRue et al. 1995; Downie et al. 1996). Typically, edges are believed to support a greater diversity and abundance of animal species compared to habitat interior (Leopold 1933; Hunter 1990). However, contradictory results have been reported with regard to the benefit of edges to communities (Morgan and Gates, 1983; Kroodsma, 1984, 1987; Bellinger et al., 1989; Yahner et al., 1989; Best et al., 1990). For example, recent reviews of studies of nest predation and brood parasitism have exposed controversial results as to whether edges are beneficial to wildlife species (Yahner and Wright, 1985; Ratti and Reese, 1988; Langen et al., 1991; Santos and Telleria, 1992), or act as "ecological traps" (Gates and Gysel, 1978; Wilcove, 1985; Angelstam, 1986; Andrén and Angelstam, 1988; Yahner and Scott, 1988; Björklund, 1990; Andrén, 1992). Furthermore, deleterious effects of edges have been documented for nesting turtles (Temple, 1987) and many plant species (Hubbell and Foster, 1986; Alverson et al., 1988), suggesting the general applicability of this phenomenon. However, a consensus may not arise because the response to edges may differ among species or biological processes (Brittingham and Temple 1983; Karieva 1987; Gascon 1993; Paton 1994; Andrén 1995; Murcia 1995).

1.2 Habitat selection in a prairie landscape mosaic

Heterogeneity created by habitat fragmentation provides new options for animals inhabiting the landscape. For example, new patches and interfaces created by fragmentation may harbour different resources, and may also bear different foraging costs or predation risk. Ultimately, an animal's choices are governed by the optimisation of its genetic fitness. Proximately, fitness is influenced by the behavioural decisions of an animal as to where to perform essential activities such as foraging and reproduction.

Selection of habitats in a fragmented landscape may occur at various scales (Johnson, 1980). For example, a first order of selection may consist of the geographical distribution of a species. Then, second-order selection may occur as the choice of a home range or territory within a geographical area. Second-order selection may affect the dynamics of populations, especially if different parts of the landscape have different benefit:cost ratios in survival or reproductive value (Pulliam 1988; Pulliam and Danielson 1991). Within the home range or territory, third-order selection consists of the distribution of foraging locations among habitats, whereas fourth-order selection addresses the use of various parts of each habitat. Both third and fourth-order habitat selection reflect the compromise an animal makes between maximising its own

fitness through foraging and reproduction, while minimizing risk of predation (Curio 1976; Lima and Dill 1990; Turner 1997). Additional orders of selection could be described with regard to prey choice, parts of prey consumed, etc. Importantly, all orders of selection reflect environmental constraints imposed on a species, and the resulting choices of an animal are directly dependent on what is available at a given spatio-temporal scale.

1.3 The North American waterfowl decline and the spatio-temporal dynamics of nest predation

The 775,000 km² Prairie Pothole Region of the northern United States and Canada produces about half of the continent's duck population annually (Smith et al., 1964). Expansion of agriculture, and the demand for more land for the production of crops or the grazing of cattle has resulted in fragmentation of numerous grasslands. Consequently, numerous wildlife taxa which rely on grasslands for reproduction or foraging activities have been declining (e.g., Askins et al. 1990). One of those wildlife groups, waterfowl, have declined throughout North America in the period 1970-1995. Ultimately, destruction and fragmentation of natural breeding habitats resulting from the expansion of agriculture has negatively impacted waterfowl communities (Herkert 1994). Proximately, predation on nests is the most important factor affecting

numerous avian populations including waterfowl (Ricklefs 1969, Böhning-Gaese et al. 1993).

On an evolutionary time scale, predation on nests is nothing new. However, changes in the structure of the landscape, notably with regard to size of remaining patches and habitat edges, may have facilitated foraging by predators, and possibly created a situation to which waterfowl are not yet adapted (Báldi 1996).

Much research has been devoted to understanding the dynamics of nest predation in relation to numerous environmental variables such as habitat characteristics (Crabtree et al. 1989), agricultural practices (Basore et al. 1986), patch size (Ball et al. 1995), distance to water (Livezey 1981) or to habitat edges (Paton, 1994; Pasitschniak-Arts and Messier 1995). However, many aspects of nest survival are highly dependent on the type of predators involved, and few studies have addressed the interactions between the ultimate and proximate causes of nest predation, i.e., the effects of habitat fragmentation on the behavioural ecology of nest predators. Knowledge of the response of nest predators to habitat fragmentation is currently insufficient to allow the complete understanding of this ecological problem.

In the parkland region of central Saskatchewan, mammalian carnivores are primary predators of duck nests, and striped skunks (Mephitis mephitis) are the most

important species (Pasitschniak-Arts and Messier 1995). The striped skunk is a small (ca. 2-5 kg) carnivore which feeds mostly on small mammals and insects (Verts 1967).

Opportunistically, striped skunks may consume songbird and waterfowl eggs (Larivière and Messier 1997a), and in some areas, predation on waterfowl nests may reach high levels (Vickery et al. 1992; Pasitschniak-Arts and Messier 1995). However, limited information is currently available on the behavioural ecology of the striped skunk (Wade-Smith and Verts 1982), especially with regards to predation on waterfowl nests. Thus, our understanding of what influences the space-use patterns of this species is critical to the understanding and mitigation of the effects of habitat fragmentation on predation of duck nests.

1.4 Objectives

My general objective was to assess the space-use patterns of free-ranging striped skunks in the Canadian prairies. To accomplish this, I captured and radio-collared striped skunks in an area highly fragmented by agriculture, and interspersed with fields managed for nesting waterfowl. Field work was conducted during the summers of 1993 to 1995. Specific objectives according to chapters are as follows.

In Chapter 2, I examine the response of striped skunks to the fragmented prairie landscape by examining their

selection of den sites. Dens play an important role in the ecology of skunks. Skunks may use dens for winter hibernation (Allen and Shapton 1942; Gunson and Bjorge 1979), parturition, rearing of offspring (Verts 1967), resting sites (Storm 1972), and occasionally to escape predators (Larivière and Messier 1996). In addition, because striped skunks rely extensively on aposematic behaviour to repel predators (Walton and Larivière 1994; Larivière and Messier 1996), inactive skunks may be more vulnerable to predation. In terms of management, den sites represent the focus of activity for females that raise young (Larivière and Messier 1997b). Thus, understanding den site selection has potential applications in terms of mitigating of waterfowl nest predation.

In Chapter 3, I examine the response of foraging striped skunks to various habitats available in a fragmented prairie landscape. Patterns of habitat selection are investigated at 3 spatial scales: 1) choice of home range within the study area, 2) distribution of foraging activity within the home range, and 3) distribution of foraging activity within large habitat patches, more specifically with regard to habitat edges. Patterns of selection are compared between sexes and among biological seasons, and are related to indices of availability of major prey, mainly insects and small mammals.

In Chapter 4, I used an experimental approach to assess whether patches of nesting habitat that contain high densities of duck nests may become ecological traps for nesting waterfowl. Reduction of suitable nesting habitats and the decrease in patch size has been suggested as attracting remaining waterfowl to nest at densities higher than in unfragmented habitats. If this is the case, then even generalist nest predators may learn to identify high-density nesting patches because of their profitability. Consequently, waterfowl may suffer density-dependent predation. To test this hypothesis, I deployed simulated waterfowl nests at various densities, and examined effects of density, nearest neighbours, and predator learning on the survival of waterfowl nests.

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2. DENNING ECOLOGY OF THE STRIPED SKUNK IN THE CANADIAN PRAIRIES: IMPLICATIONS FOR WATERFOWL NEST PREDATION

2.1 Introduction

Waterfowl and songbird populations have been declining throughout North America since the 1970s (Bethke and Nudds 1995; Rodenhouse et al. 1992; Kantrud 1993). Ultimately, destruction and fragmentation of natural breeding habitats, especially North American grasslands (Knopf 1988; McNicholl 1988), is responsible for the decline of both avian groups (Bethke and Nudds 1995; Böhning-Gaese et al. 1993; Herkert 1994). Proximately, predation on nests is the most important factor affecting songbird and waterfowl numbers (Klett et al. 1988; Johnson et al. 1989; Ricklefs 1969).

To enhance nesting success of North American waterfowl, numerous management programmes such as enhancement of upland nesting cover (Crabtree et al. 1989), deployment of safe nesting structures (Norman and Riggert 1977), erection of exclosures against terrestrial predators (LaGrange et al. 1995), and control of predators on specific areas (Sargeant et al. 1995; Beauchamp et al. 1996) have been employed with varying degrees of success. However, our ability to mitigate nest predation is currently impaired by our lack of knowledge on the behavioural ecology of carnivores preying on waterfowl nests.

The striped skunk Mephitis mephitis is a small (ca. 2-5 kg) carnivore which feeds mostly on small mammals and insects (Verts 1967). Opportunistically, striped skunks may consume songbird and waterfowl eggs (Larivière and Messier 1997a), and in some areas, predation on waterfowl nests may reach high levels (Vickery et al. 1992; Pasitschniak-Arts and Messier 1995).

In temperate regions, parturition in striped skunks occurs around 15 May, and altricial young are born fully-furred, toothless, and with eyes closed. Males do not provide parental care, and adults are solitary (Larivière and Messier 1997b). Young skunks remain at the maternal den until early July (ca. 45 days) when they start to accompany their mother during foraging trips (Larivière and Messier 1997b). Thus, during most of the waterfowl nesting season (ca. May 15-July 15), female skunks display fidelity to a maternal den where their progeny is located (Larivière and Messier 1997b). The location and characteristics of these denning sites may have a significant impact on the survival of nearby waterfowl nests, and den site management may provide managers with non-destructive ways of managing predators of waterfowl nests.

I investigated the patterns of den site selection by striped skunks during the waterfowl nesting season. More specifically, I tested the following null hypotheses: 1) maternal dens are randomly distributed among habitats, 2)

habitat preferences with regard to resting sites and maternal dens do not differ, and 3) characteristics of resting sites do not differ between males and females. Finally, I discuss how my findings can be applied to the management of the striped skunk as a predator of waterfowl nests.

2.2 Materials and methods

2.2.1 Study area

This study was conducted in the aspen parkland region of southcentral Saskatchewan (52°45' N, 107°08' W), Canada. The area is dominated by farmland, and interspersed with numerous wetlands and stands of trembling aspen Populus tremuloides. Fields managed specifically as nesting cover for upland nesting waterfowl are common throughout the area. Topography is gently rolling, and an extensive network of grid roads provides access to the land.

2.2.2 Livetrapping

From April to June, 1993-1995, striped skunks were livetrapped around areas of managed waterfowl nesting cover. Captured skunks were anaesthetized with halothane and Telazol® (Larivière and Messier 1996b, 1996c), and equipped with motion-sensitive radio-collars possessing a 5-sec delay activity switch (Telonics Inc., Mesa, Arizona, USA). Skunks were handled and released at the site of

capture. I followed a university-approved animal welfare protocol (#920091) while conducting this research.

2.2.3 Radio-tracking

From April to August, 1993-1995, I located radio-collared skunks once a week during daytime hours (9.00 - 16.00 h CST) when skunks are inactive (Larivière and Messier 1997b). In addition, night-time resting sites were recorded during over 2268 hours of radio-tracking. The location of each animal was determined by homing on the radio signal with portable telemetry equipment until the den site or retreat was discovered. Physical characteristics of den or resting sites were recorded, including den type (underground burrow, building, culvert, or above-ground retreat), habitat type, and size and orientation of burrow entrances.

2.2.4 Identification of maternal dens

I defined as "maternal den" any retreat for which at least two of the following criteria were satisfied: fidelity of use for >3 consecutive days during the parturition/rearing period, collection of grass for preparation of the nest chamber (Allen 1939; Allen and Shapton 1942), and presence of young during the rearing period. Females may prepare and use more than one den before and during the parturition/rearing period, and I

considered all maternal dens in my analyses. The selection of maternal den or nest sites is under strong evolutionary pressure because it directly affects the fitness of individuals (Martin 1995). Thus, I assumed that the choice of each maternal den by female skunks was independent of previous choices, and of the choice of other female skunks.

2.2.5 Habitat classification and availability

Habitats were classified from ground-proofed aerial photographs in the following seven exclusive categories: 1) wetland, 2) managed nesting area, 3) farmstead, 4) right-of-way, 5) woodland, 6) cropland, and 7) miscellaneous habitats. Wetland habitat consisted of the band of vegetation surrounding open water in permanent, semi-permanent, and temporary wetlands. Managed nesting areas consisted mostly of uncut hayfields, natural grasslands, and dense nesting cover; fields of dense nesting cover were not cut, and were sown primarily with alfalfa, brome, and crested wheatgrass to create prime habitat for nesting waterfowl. Farmstead habitat included mostly abandoned farmsteads and other aggregations of abandoned buildings. Rights-of-way were narrow (<5 m wide) ditches of native and non-native grasses, shrubs, and occasionally trees bordering gravel and paved roads. Woodland consisted of stands of trembling aspen, balsam poplar *P. balsamifera*, and various shrubs such as willows *Salix* spp., rosebushes

Rosa spp., buckbrush Symphoricarpos occidentalis, wolf willow Elaeagnus commutata, and buffalo berry Shepherdia argentea. Cropland was typically seeded, harvested, and cultivated yearly with mostly small grain (e.g. wheat, barley, rye, and oats) and oil crops (e.g. canola and flax). Other less common crops included peas, lentils, buckwheat, and canary seeds. Miscellaneous habitats consisted of small or linear habitats excluded by previous categories such as fencelines, rockpiles, and grazed pastures.

Availability of each habitat type was assessed from a digital map of the study area using a Geographical Information System (SPANS). The study area consisted of all sections of land (ca. 2.5 km²) used by radio-collared skunks (ca. 220 km²). Overall, habitat availability was computed for the entire study area to assess habitat preferences at the population level (Manly et al. 1993). Sample sizes per skunk for resting sites were too small to assess habitat selection patterns within individual home ranges.

2.2.6 Statistical analyses

Patterns of habitat selection for maternal den sites were determined using Chi-Square goodness-of-fit analysis (Neu et al. 1972) and Bonferroni confidence intervals (Byers et al. 1984). This analysis is appropriate because

1) availability of each habitat was precisely known through GIS spatial analysis, and 2) I considered all maternal dens simultaneously, and contrasted their use within the mosaic of habitats available throughout the study area (design 1, Thomas and Taylor 1990).

I used a different approach for investigating habitat preferences for resting sites. Striped skunks often rest while foraging (Larivière and Messier 1997b), and choice of habitat may reflect foraging preferences. However, striped skunks typically use only one retreat per night (range = 0-2, Larivière and Messier 1997b). Therefore, I considered each retreat as independent. In addition, I considered each animal separately in my analysis, and only considered data from skunks for which I obtained ≥ 12 retreats and enough locations to determine home range size (i.e. ≥ 40 locations, see Larivière and Messier 1998). Availability of each habitat was determined for each skunk at the home range level (third-order selection, Johnson 1980). Because the sample of resting sites for each animal was relatively low (range = 12-27), I used a Friedman repeated measures analysis of variance on ranks to assess habitat preferences. Since Friedman test ranks all habitats, it is less sensitive to extreme absolute differences. Furthermore, the test gives equal weight to all individuals, which puts the emphasis on population trends, not individual differences. Water was excluded from all

habitat calculations. All statistical procedures were performed using two-tailed probability levels, and P values ≤ 0.05 were considered significant. Values are reported as mean \pm SE unless stated otherwise.

2.3 Results

In total, 46 skunks (34 F, 12 M) were captured, and denning information was obtained for 32 females and 8 males which were radio-tracked during over 2268 hours. Radio-tracking effort was systematically distributed among all skunks, and on average, individual skunks were radio-tracked 1-3 nights per month from April to August (see Larivière and Messier 1997b). Only four females were radio-tracked during more than one year: three females were tracked in 1994 and 1995, and one female was tracked in 1993 and 1995.

2.3.1 Maternal dens

Thirty of 32 females used at least one maternal den. Two adult females captured approximately one month after parturition (12 June 1993 and 24 June 1994, respectively), did not exhibit any maternal behaviour or display den site fidelity when radio-tracked, even though they were lactating when captured. All other females exhibited strong den site fidelity, thus indicating the presence of a litter in the den. From 1993-1995, 47 different maternal dens were

used 57 times.

Throughout the parturition and rearing period, 20 females prepared or used only one maternal den, whereas 9, 2, 2, and 1 females used two, three, four and five maternal dens, respectively (median = 1, range = 1-5, \bar{n} = 34). Maternal dens (\bar{n} = 47) were either underground burrows (55%) or holes underneath buildings (45%, Fig. 2.1). Ten maternal dens were reused by the same or by different females over the three summers: 9/10 maternal dens reused were buildings in farmsteads, and one was an underground burrow in a right-of-way.

2.3.2 Habitat preferences for maternal dens

Cropland was highly available (66%) and never used for maternal dens. Thus, I excluded cropland from the analysis to eliminate potential biases by forcing preferences to all other habitats (Johnson 1980). The forty-seven maternal dens were not distributed randomly among habitats (χ^2 = 294, df = 5, P < 0.01; Fig. 2.2). Farmsteads were the only preferred habitat, whereas managed nesting areas and woodland were avoided. All other habitats were neither selected nor preferred (Fig. 2.2).

2.3.3 Chronology of den use and switching of maternal dens

Twenty females used only one maternal den. Females started showing fidelity to their respective den site as

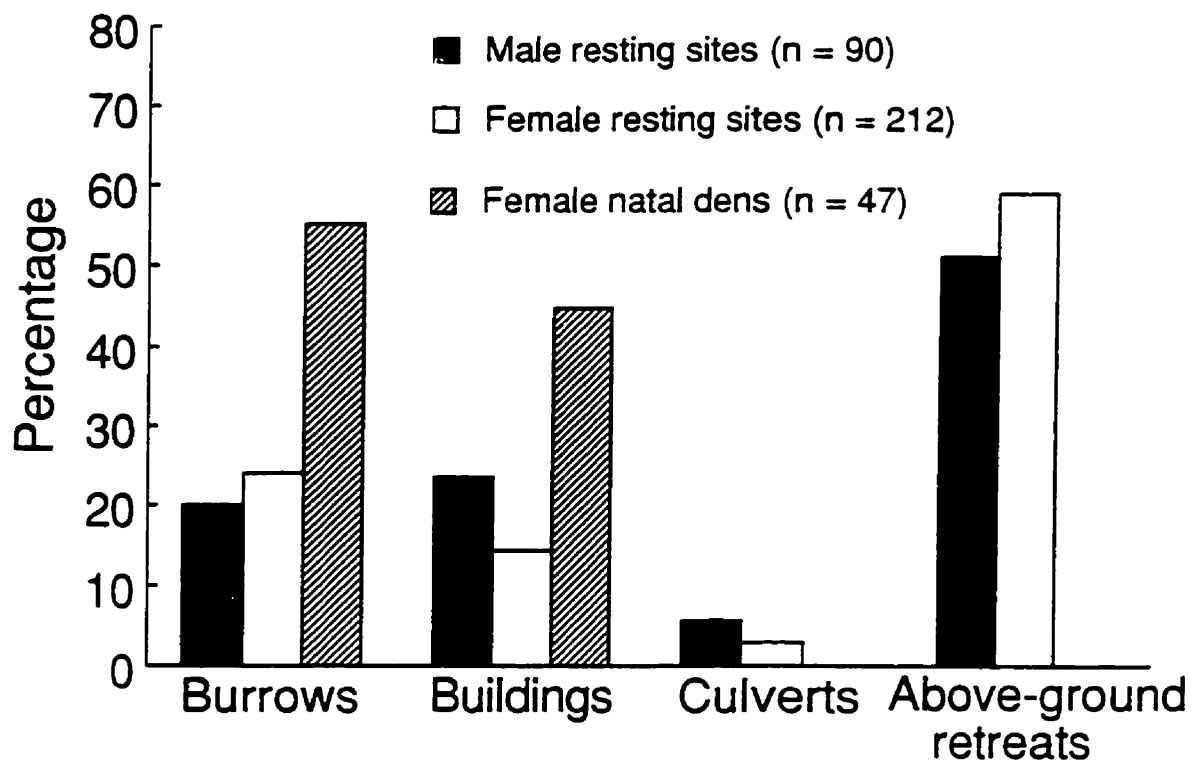


Figure 2.1. Types of retreats used by striped skunks in Saskatchewan, Canada, 1993-1995.

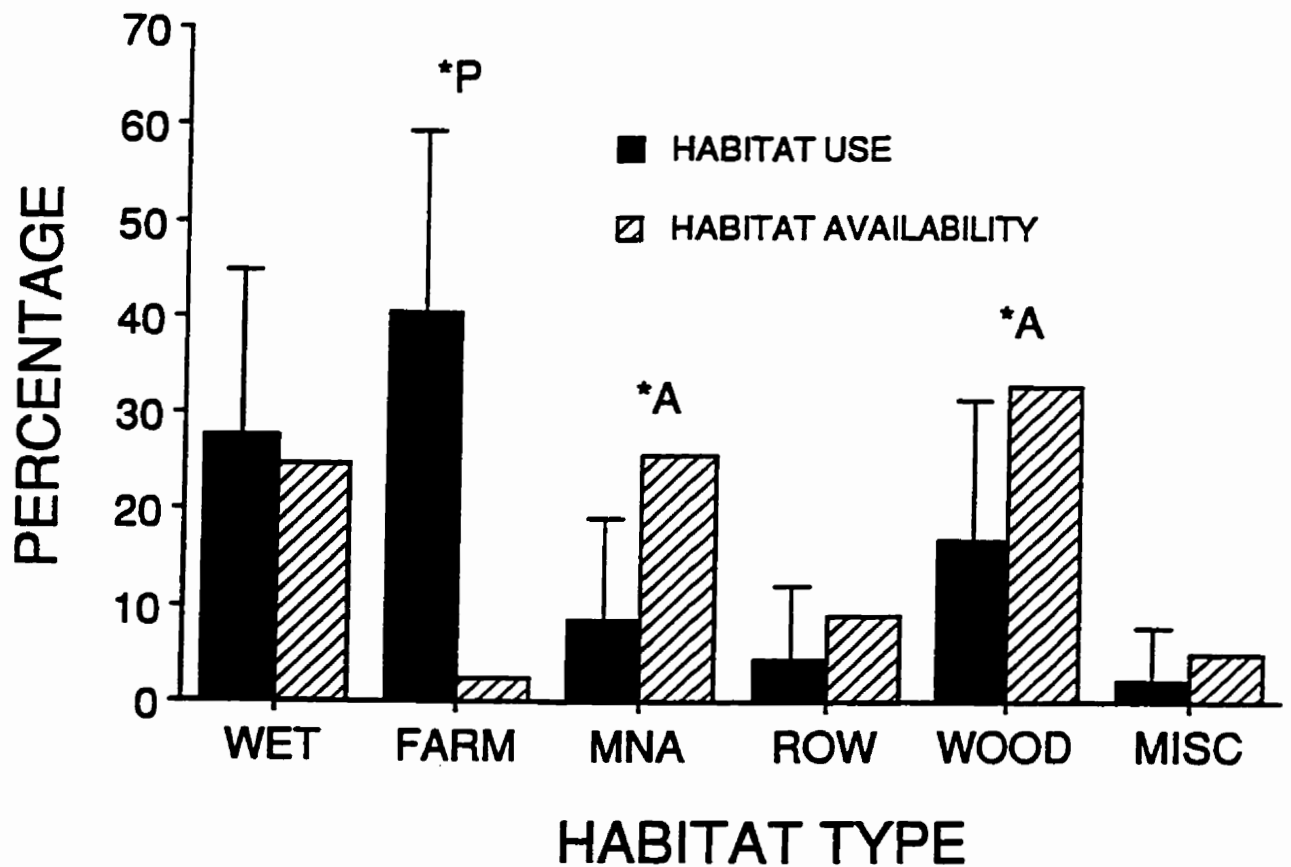


Figure 2.2. Habitat preferences indicated by 47 natal den sites used by 30 female striped skunks in southcentral Saskatchewan, Canada, 1993-1995. Cropland was excluded from this analysis. Habitat types are: wetlands (WET), farmsteads (FARM), managed nesting areas (MNA), right-of-ways (ROW), woodland (WOOD), miscellaneous habitats (MISC), and cropland (CROP). Error bars represent Bonferroni intervals. *P and *A indicate habitats significantly preferred and avoided, respectively.

early as 17 April, and continued to do so as late as 7 July, a period covering 81 days. If only skunks that were captured before 15 May (approximate parturition date) and that were radio-tracked throughout the entire summer ($\underline{n} = 8$) are considered, the mean occupation time is 47 ± 3 days.

Fourteen females used >1 maternal den. Mean occupation time was 60 ± 3 days ($\underline{n} = 10$), which was significantly greater than that of females using a single den (Mann-Whitney U test, $n_1 = 8$, $n_2 = 10$, $Z = -2.62$, $\underline{p} < 0.01$). I have no evidence that females changed maternal dens as a response to observer visits. However, one female relocated her progeny >2 km away after being captured (13 July 1993) just outside her den in a trap set for Richardson ground squirrels Spermophilus richardsonii. Her second location was not considered in my analyses.

2.3.4 Sharing of maternal dens

Spatial distribution of maternal dens suggests that females do not defend the immediate area around their maternal dens, as I observed two females using maternal dens that were <10 m apart (relatedness of both individuals was unknown). Within one year, two maternal dens were consecutively used by two different females. Finally, two maternal dens were also used as resting sites by other females outside the parturition/rearing period. However, simultaneous sharing of the same dwelling by two

individuals was never observed.

2.3.5 Reuse of maternal dens

In my area, striped skunks experienced ca. 40% mortality during the summer (Larivière and Messier 1998). Thus, only 4 females were radio-tracked during more than one year. Two of three females tracked in 1994-1995, and one female tracked in 1993 and 1995 reused the same maternal den. These data suggest that females regularly used the same maternal den during consecutive years.

2.3.6 Characteristics of resting sites

I collected information on 428 resting sites. However, exact type of retreat could not be determined for 126 resting sites for fear of disturbance during radio-tracking sessions. No difference could be detected between sexes in the proportion of each type of resting site used ($\chi^2 = 5.6$, $df = 3$, $p = 0.13$; Fig. 2.1). Overall, resting sites ($n = 302$) were mostly above-ground retreats (57%), underground burrows (23%), and buildings (17%). Above-ground retreats consisted simply of any place, usually in thick understory, where skunks would rest or sleep without preparing a nest or altering the surroundings. Dry culverts comprised 3% of retreats used.

Size of entrances of underground burrows varied from 6.5 cm to 45 cm, and differed ($t = 3.0$, $df = 81$, $p < 0.01$)

between burrows used by males (25 ± 2 cm, $\underline{n} = 15$) and females (18 ± 1 cm, $\underline{n} = 68$). Because underground burrows are dynamic structures which may be used and modified by sympatric species (Verts 1967), I did not attempt to determine the origin of every underground burrow used by striped skunks. Nonetheless, I believe that most burrows used by skunks were dug by skunks, coyotes Canis latrans, North American badgers Taxidae taxus, red foxes Vulpes vulpes, muskrats Ondatra zibethicus, and North American beavers Castor canadensis. Den openings faced primarily southeast, and did not differ between resting sites and maternal dens (Watson F-test for 2 circular means, $\underline{F} = 1.7$, $\text{df} = 85$, $\underline{P} = 0.20$).

2.3.7 Habitat preferences for resting sites

I analyzed 108 and 320 resting sites for males and females respectively. Distribution of resting sites was not homogenous among habitats for either males ($\underline{F}_r = 16.0$, $\underline{n} = 5$, $\underline{k} = 7$, $\underline{P} = 0.01$) or females ($\underline{F}_r = 39.4$, $\underline{n} = 10$, $\underline{k} = 7$, $\underline{P} < 0.01$). Both sexes displayed a strong avoidance of cropland, and a definite preference for wetlands and farmsteads relative to other habitats (Fig. 2.3).

2.3.8 Sharing of resting sites

While some sites were reused by the same or by a different skunk, I never observed skunks sharing a resting

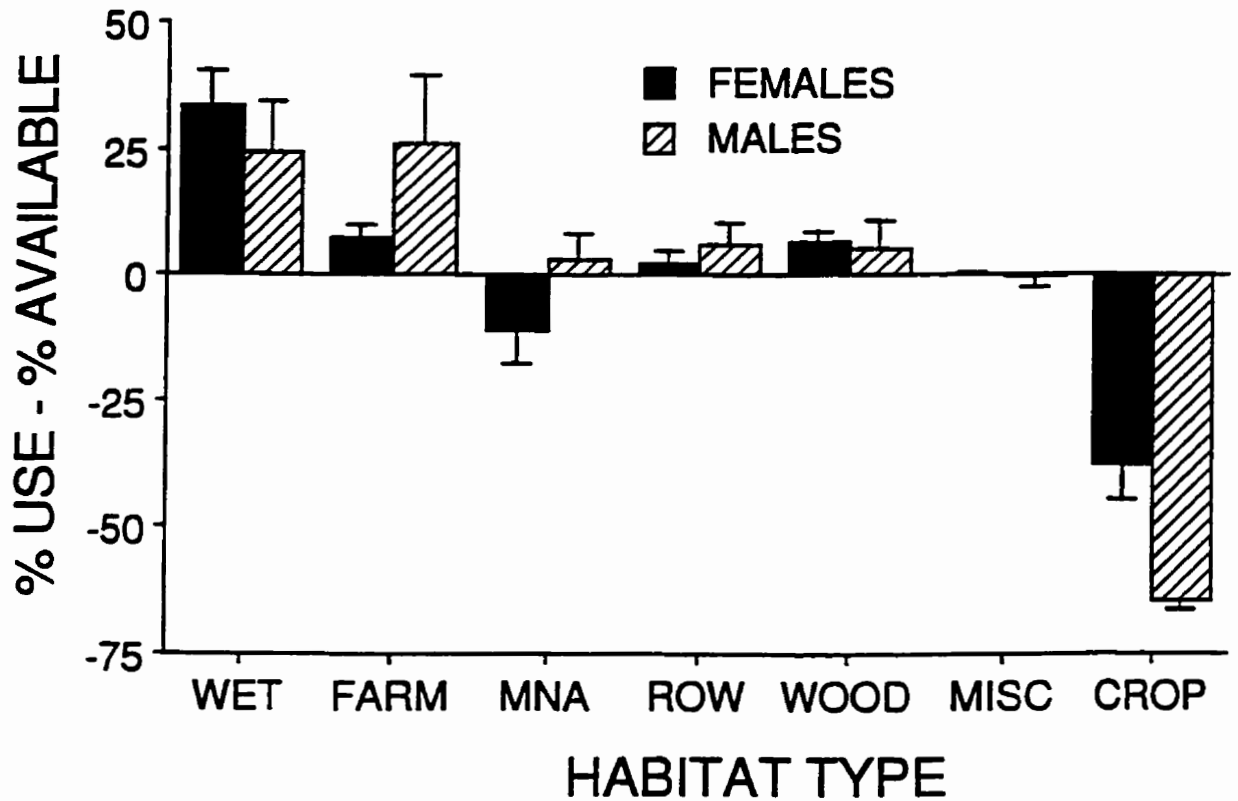


Figure 2.3. Habitat preferences indicated by 88 resting sites used by 5 males, and by 176 resting sites used by 10 female striped skunks in southcentral Saskatchewan, Canada, 1993-1995. Habitat types are: wetlands (WET), farmsteads (FARM), managed nesting areas (MNA), right-of-ways (ROW), woodland (WOOD), miscellaneous habitats (MISC), and cropland (CROP). Error bars represent the standard error of the mean for each value.

site simultaneously. Because of the large numbers of retreats used, and because resting sites recorded by one observer were unknown to other observers (and during other years), I did not attempt to assess reuse of resting sites. Nonetheless, I have indications that some resting sites were reused by members of both sexes. However, most cases (>95%) of reuse of resting sites involved human structures (buildings) or equipment (farm machinery, tin buckets, metal pipes, and tyres).

2.4 Discussion

The striped skunk is an important predator of waterfowl nests (Pasitschniak-Arts and Messier 1995; Larivière and Messier 1997a). Because females reach higher density, have overlapping home-ranges, and use their home ranges more intensively than males, females have been identified as the sex of concern with regard to nest predation (Larivière and Messier 1998). In my study, female skunks were 1) selective in their choice of habitats for maternal dens, 2) more selective in their choices of maternal dens than resting sites, and 3) did not exhibit different preferences for resting sites when compared with males.

Female striped skunks exhibit fidelity to the maternal den through most of the waterfowl nesting season (Larivière and Messier 1997b). In this study, I obtained evidence that

prime sites for maternal dens may be used by several females and are reused from year to year. In addition, females do not defend territories, and several den sites may be in close proximity. Thus, good denning areas may concentrate much of the foraging activity of resident female striped skunks. Because survival of duck nests typically increases with distance from the nest or den of a predator (Shields and Parnell 1986; Sullivan and Dinsmore 1990), identification of maternal den sites may be useful in identifying areas of high predator activity where waterfowl nests are most at risk.

Striped skunks made extensive use of buildings for maternal dens and resting sites. Mammals such as pine martens Martes americana (Spencer 1987), stone martens M. foinea (Lachat Feller 1993), and polecats Mustela putorius (Weber 1989), also use human-made structures as shelters. In my study, striped skunks occupied farmsteads where human use was minimal (mostly limited to storage of equipment and grain). Thus, farmsteads may be selected mostly for the presence of buildings and the absence of human activity. Whilst abandoned farmsteads may also be used by potential predators such as coyotes and North American badgers, buildings may reduce predation risk by providing physical barriers against these larger predators. Furthermore, buildings offer both low construction and maintenance costs, and may provide thermoregulatory advantages (see

Weber 1989) which may be critical for juvenile striped skunks during the long (up to 12 h) foraging trips of females during the rearing period (Larivière and Messier 1997b). In this respect, females sometimes use grass plugs at the entrance of their burrows (this study; see also Allen 1939). Thermoregulation may also explain preferences for burrows which face away from the prevailing north-west wind. The larger size of male burrows (38% larger) probably reflects the larger body mass of male skunks (26% heavier, Larivière and Messier 1996c).

Preference of wetlands for resting sites may reflect greater use of these habitats for foraging (Chapter 3). Skunks often rest near food sources (Larivière and Messier 1997a), and may rest in high prey abundance habitat when performing sit-and-wait foraging (Crabtree et al. 1989).

Striped skunks perform neither scent marking nor territorial defence (Verts 1967; Larivière and Messier 1997b). In this study, striped skunks were never observed to mark their burrows, although the strong natural body odour of skunks (Larivière and Messier 1996a) may be sufficient to advertise occupancy of den sites. Simultaneous sharing of resting sites was not observed in my study, and is generally rare (Storm 1972). Limited evidence suggests that females may defend access to their maternal dens against males and possibly against other females (Larivière and Messier 1998).

More than 40% of my radio-collared female skunks ($n = 30$) switched maternal dens. Den switching by mammalian females may occur in response to build-up of parasites (Butler and Roper 1996), for sanitary reasons (striped skunk often excrete inside their burrows, Allen 1939; Verts 1967), to avoid attracting predators by accumulating prey remains (Prestrud 1992), to relocate closer to food sources, or following human disturbance (Goodrich and Berger 1994). However, striped skunks are extremely tolerant of predatory and non-predatory disturbances (Walton and Larivière 1994; Larivière and Messier 1996a), and I believe my research activities did not induce den switching. Furthermore, food depletion is unlikely to explain den switching by females as prey of skunks (mostly insects and small mammals) are both generally abundant and rapidly renewable over time. Because striped skunks do not carry prey remains to their progeny, it is also unlikely that den switching was stimulated by the presence of prey remains. Accumulation of skunk faeces inside the den (Verts 1967) and possible build-up of parasites (Butler and Roper 1996) are thought to be the most plausible explanations for den switching. In my study, females that used a single den had shorter occupancy periods, which may provide indirect support for this hypothesis. However, data are currently unavailable to examine what induces switching of maternal dens in female skunks.

Striped skunks display den preferences for human structures (e.g. buildings). Removal of potential denning sites from the proximity of nesting areas may lead to a more uniform distribution of female activity, and prevent localized concentration of striped skunks. However, because of their flexibility in denning habits, and the capacity to dig their own burrows, it is unlikely that densities of striped skunks are limited by the availability of den sites, as was found for the American mink Mustela vison in the United Kingdom (Halliwell and Macdonald 1996). In fact, numerous farmsteads and buildings which were present in my study area were not used by skunks. Thus, all farmsteads and buildings may not have the same ecological value as maternal den sites for striped skunks. However, the high degree of preference displayed by female striped skunks for abandoned farmsteads and buildings is unequivocal, and management of maternal den sites such as buildings may provide researchers with a non-destructive avenue to predator management that is less expensive and controversial than predator exclusion or removal.

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3. RESTORED GRASSLANDS, HABITAT EDGES, AND STRIPED SKUNKS: MULTISCALE PATTERNS OF HABITAT SELECTION BY A PREDATOR OF WATERFOWL NESTS.

3.1 Introduction

North American grasslands, with their high abundance of wetlands and vast expanses of short and tall-grass prairies, provide high-quality nesting habitat for numerous bird species (Knopf 1988). However, the expansion of agriculture in the prairies has led to the destruction and fragmentation of numerous grasslands (Knopf 1988; McNicholl 1988). Consequently, there have been declines of some waterfowl and songbird species since the 1970s (Bethke and Nudds 1995; Rodenhouse et al. 1992; Kantrud 1993).

For numerous avian species including waterfowl, predation on nests is the most important proximate factor affecting populations (Böhning-Gaese et al. 1993; Klett et al. 1988; Ricklefs 1969), and many adaptations have evolved to counteract predation on nests (Lack 1968). However, rapid changes to the environment, caused by expansion of agriculture and resulting fragmentation of natural habitats, may represent a situation to which North American waterfowl are not yet adapted (Báldi 1996). In particular, the current high rates of nest predation may be explained by the response of predators to fragmented habitats. There is little information on how nest predators respond to habitat fragmentation (Robinson et al. 1995), or to habitat edges (Andrén 1995; Paton 1994).

In response to destruction of natural grasslands, several conservation programs have been established to preserve remaining native grasslands and convert cropland to "restored" grasslands suitable for duck nesting. The latter strategy consists of seeding and maintaining cultivated land with native and tame grasses (e.g., Blankespoor 1980). Several such projects have been established throughout the USA (e.g., Conservation Reserve Program, Waterfowl Production Areas) and in Canada (e.g., Managed Nesting Areas). Soil banks, wetlands, and waterfowl are often the target of such management programmes, but the overall benefits extend to numerous wildlife taxa (Hall and Willig 1994; Hartley 1994; Johnson and Schwartz 1993; Kantrud 1993). From an ecological standpoint, restored grasslands may act as ecological traps: not only may such habitats attract more nesting birds, they may also attract more predators (Rich et al. 1994). Furthermore, smaller patches have more edge per unit area compared to larger patches. So far, no studies have addressed the use of restored grasslands by nest predators in light of the controversy as to whether edges are beneficial to wildlife (Yahner and Wright 1985; Ratti and Reese 1988; Storch 1991), or act as ecological traps (Gates and Gysel 1978; Temple 1987; Andr  n and Angelstam 1988).

The striped skunk is a small (ca. 2-5 kg) carnivore which feeds mostly on small mammals and insects (Verts

1967). Opportunistically, skunks prey on songbird and waterfowl nests (Larivière and Messier 1997a; Vickery et al. 1992) and, in some areas, predation by skunks on waterfowl nests may be extensive (Crabtree and Wolfe 1988; Pasitschniak-Arts and Messier 1995). Because the striped skunk is an important nest predator throughout North American prairies (Johnson et al. 1989), I used this species as a model for testing the response of predators to managed nesting areas and habitat edges. More specifically, I tested the following null hypotheses: 1) striped skunks use restored grasslands in proportion to their availability, 2) patterns of habitat selection do not vary between sexes, or among biological seasons, 3) patterns of habitat selection of striped skunks are independent of the availability of their major prey, namely insects and small mammals, and 4) patterns of habitat selection are independent of habitat edges.

3.2 Materials and methods

3.2.1 Study area

This study was conducted in southcentral Saskatchewan, Canada (52°45' N, 107°08' W). The area (ca. 220 km²) is dominated by farmland, and interspersed with numerous wetlands and stands of trembling aspen. Cropland represents 66% of the area, and is mostly used for the production of small grain (e.g., wheat, barley, rye, and oats), and oil

crops (e.g., canola and flax). Other less common crops include peas, lentils, buckwheat, and canary seeds. Woodland and managed nesting areas occupy 11% and 9% of the landscape, respectively. Managed nesting areas consist mostly of dense nesting cover, hayland, and idle pastures. Fields of dense nesting cover are sown with alfalfa, brome, and crested wheatgrass to create prime habitat for nesting waterfowl. Small or linear habitats such as wetlands, rights-of-way, farmsteads, and miscellaneous habitats represent 8%, 4%, 1%, and 1% of the land available, respectively. Topography is gently rolling, and the land is divided by an extensive network of grid roads.

3.2.2 Trapping

In 1993, striped skunks were livetrapped at two sites, Redberry and Postnikoff, each ca. 25 km² and centered on a quarter section (0.6 km²) of managed nesting habitat (Fig. 3.1). In 1994, Redberry was used again, but Postnikoff was replaced by another site, Boulanoff. Each study area was chosen on the basis of a high availability of managed nesting cover, and low abundance of wooded areas in order to facilitate radio-tracking by observers on foot. Trapping effort was evenly distributed between sites. Captured skunks were anesthetized with halothane and Telazol[®] (Larivière and Messier 1996a, 1996b), and equipped with motion-sensitive radio-collars (Telonics Inc., Mesa,

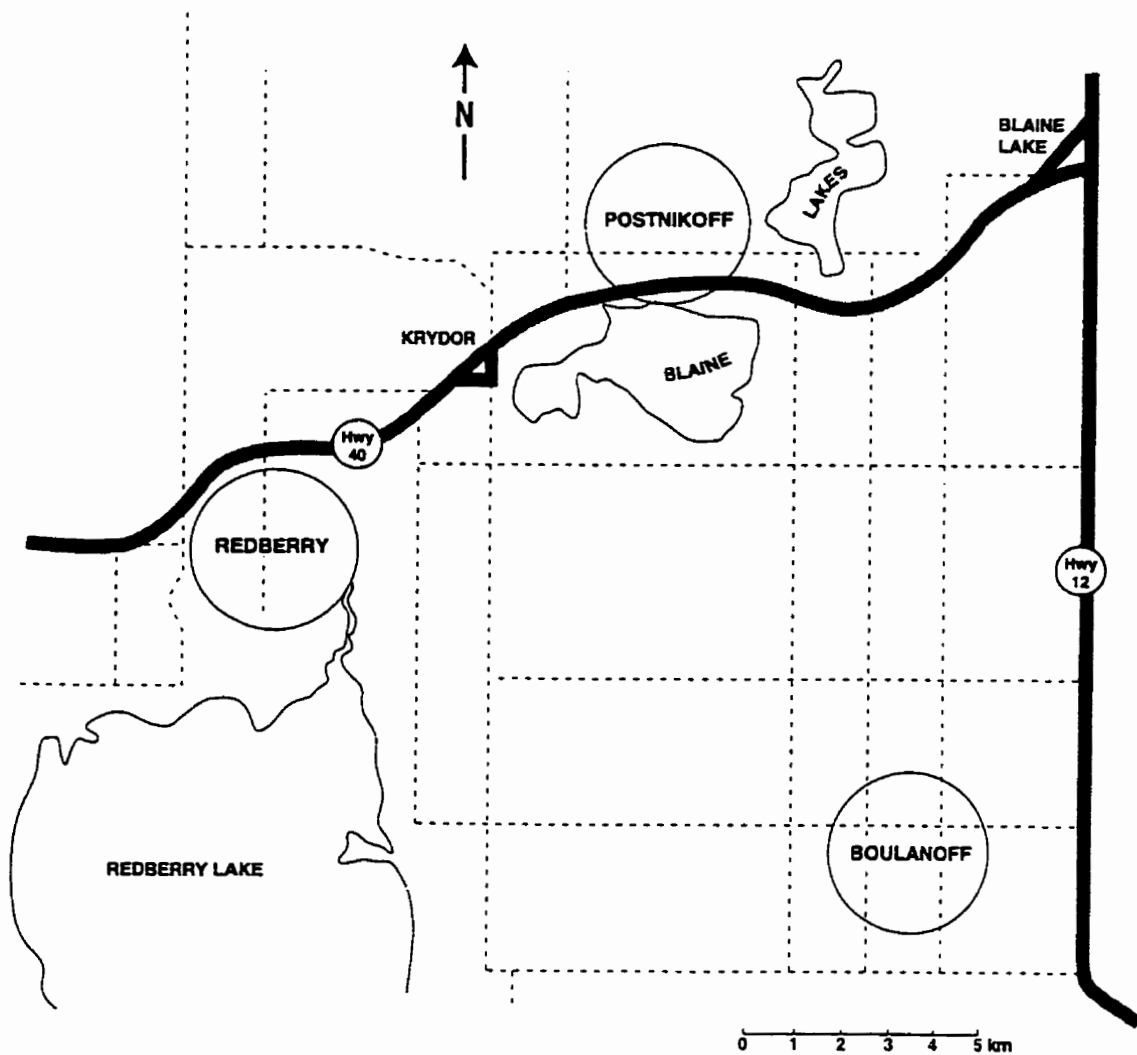


Figure 3.1. Geographic distribution of trapping sites for striped skunks in the Thickwood Hills, Saskatchewan.

Arizona). Skunks were handled and released at the site of capture.

3.2.3 Radio-tracking

Radio-collared animals were located by a single observer on foot from 18:00 to 06:00, during the period of greatest activity (Larivière and Messier 1997b). I used night-vision equipment to directly observe skunks during tracking sessions. Tracking effort was systematically distributed among all skunks, and no animal was tracked during two consecutive nights. Locations immediately following an observer-induced defensive posture (Larivière and Messier 1996c) were discarded from analyses due to possible observer disturbance.

Individuals were located every 15 min by direct observation, auditive location, or short-range (<50 m) triangulation (Appendix A). For each location, I recorded habitat type in one of the following seven exclusive categories: 1) wetland (riparian terrace, wetland margin, or any terrestrial component included in a wetland complex -- WET), 2) managed nesting area (MNA -- including delayed hay cuts, idle pastures, and dense nesting cover sensu Pasitschniak-Arts and Messier 1995), 3) farmstead (either active or abandoned -- FARM), 4) rights-of-way (ROW), 5) woodland (WOOD), 6) cropland (CROP), and 7) miscellaneous habitat (fencelines and rockpiles -- MISC).

In addition, I recorded the distance to the nearest edge by pacing for distances <50 m (1 step = 1 m), and estimated to nearest 10 m for distance >50 m. Availability of each habitat type and edge categories was determined from spatial analysis of photo maps in SPANS™ GIS. Edge distances were categorized as 0-25 m, 26-50 m, 51-100, and >100 m.

The study area was delineated by all sections of land on which I located one of my radio-collared skunks during tracking sessions. Areas covered by each habitat type (excluding areas of water) were calculated for each study site (i.e., Boulanoff, Redberry, and Postnikoff), and for individual home ranges (100% minimum convex polygon -- Larivière and Messier 1998) in order to assess habitat preferences within the study area and within home ranges (i.e., second and third order selection; Johnson 1980).

Availability of area for each edge category was assessed for individual home ranges (100% minimum convex polygon, Larivière and Messier 1998), and cross-tabulated with habitat type using GIS. Because edge effects are habitat dependent (Andrén 1995), availability of edge categories was determined within habitat (fourth-order selection). In my study area, most wetlands were potholes of small size (<5 ha), and occurred as remnant patches surrounded by a narrow (<10 m) ring of cattails (Typha sp.), willows (Salix sp.), or trembling aspen. Ring zones

(sensu Forman and Godron 1981) offer narrow buffers between water and cropland, and may be comprised entirely of edge habitat. Thus, I excluded small or linear habitats (14% of study area), and only considered habitats that were large enough to contain a significant proportion of habitat interior: managed nesting areas, woodland, and cropland.

Our radio-tracking schedule was intensive (i.e., locations every 15 min), and designed to maximize direct behavioural information instead of statistical independence within an animal's home range (Swihart and Slade 1985). Using Shoener's ratio, I estimated that, at the home range level, statistical independence between locations occurred at intervals ≥ 270 min. However, striped skunks are highly mobile, and are capable of moving >1 km in 15 min, even in dense vegetation (Appendix A; Verts 1967). Because of the small size of even the largest habitat patches in my study area (maximum patch size = 0.64 km^2), and considering that a skunk could easily access several other habitats (and edge categories) within the 15-min sampling interval, I estimated that movements reflected behavioural decisions by individual skunks, not physical constraints. Thus, each location was considered independent for my analyses of third and fourth order selection (i.e., selection at the individual level). Biological seasons for striped skunks were previously identified (Larivière and Messier 1997b) as pre-parturition (April-May 14), parturition/rearing (May

15-June 30), pre-dispersal (July), and dispersal (August).

3.2.4 Prey abundance

In 1994, I sampled the relative abundance of prey (insects and small mammals) in each habitat to further understand the factors explaining the patterns of habitat selection in striped skunks. More specifically, I investigated whether the use of specific habitats by skunks is correlated to their respective abundance of prey.

Sampling of insect abundance at each sampling station consisted of three transects running at 5, 35 and 75 m from the nearest habitat edge. In small or linear habitats (e.g., wetlands, woodland, rights-of-way), sampling was performed by running the transect back and forth between the boundaries, thus covering all edge distances. Each transect was 25 m long, and sampled by sweep sampling, at the rate of 1 sweep/pace (1 pace = 1 m). Four sampling stations were permanently positioned in a different patch of each habitat type, and were reused for all months (May-August). For each habitat, all sampled patches ($n = 3$ per habitat) were separated by ≥ 1 km, and thus, I considered the patch as the sampling unit. No sampling was performed in miscellaneous habitats. Sampling was executed ca. the 15th of each month, during rainless nights. In order to sample the species which may be available to the skunks, sampling started at 2200 h and typically lasted until 0400

h. An index of insect abundance was obtained by measuring the fresh biomass (g) of insects collected for each transect. Only the orders Coleoptera, Hymenoptera, and Orthoptera were considered as they represent the three orders most commonly consumed by skunks (Verts 1967).

Small mammal abundance was estimated during three days of snap-trapping performed the 14th - 16th of each month. Each transect consisted of 16 pairs of snap traps separated by 10 m and running from the edge towards the habitat interior. Four transects were permanently established in three different patches of each habitat. All species of small mammals were included in my calculations, but I excluded ground squirrels (Spermophilus sp.) and northern pocket gophers (Thomomys talpoides) which are not commonly consumed by striped skunks (Verts 1967). Relative abundance of small mammals was measured as the number of small mammals captured per 100 trap nights. My objective was not to estimate the absolute density of small mammals and insects in each habitat, but instead to provide a simple means of ranking habitat types according to their relative abundance of prey. Because all transects in all habitats were covered the same night, biases in prey abundance due to weather factors remained the same for all habitats.

3.2.5 Statistical analyses

Habitat selection patterns were determined at three

spatial scales: 1) habitat composition of home ranges within the study area, 2) locations of striped skunks within individual home ranges, and 3) use of habitat edges within specific habitat types. I used each animal as a sampling unit, and estimated selection patterns using compositional analysis (Aebischer et al. 1993) to alleviate the problems of non-independence among radio-locations (Aebischer and Robertson 1992). A multivariate analysis of variance (Λ -statistic) was used to test the effects of sex, and biological seasons on patterns of habitat selection.

I tested for differences in the relative insect and small mammal abundance among months and habitats using a two-way repeated measures analysis of variance on log-transformed data. Replicates (e.g., patches; $n = 4$ for insects, and $n = 3$ for small mammals) were considered as independent, and used as sampling units for each habitat type. Multiple comparisons were performed using Tukey's Studentized Range Test to control the experiment-wise error rate. Habitat preferences and prey abundance were compared using non-parametric Spearman rank-order correlation. Statistical procedures were performed using two-tailed probability levels, and P values ≤ 0.05 were considered significant.

3.3 Results

During 1993 and 1994, 41 striped skunks (11 M, 30 F)

were captured and radio-collared. Because of high mortality (39%, $n = 41$ skunks), and dispersal of males outside the study area (45%, $n = 11$) during the summer (May-August), I radio-tracked 36 skunks (8 M, 28 F) for 1,873 h and obtained home range information for 26 striped skunks (5M, 21F). Spatial organization and home range characteristics are reported elsewhere (Larivière and Messier 1998). In total, 3,392 habitat-specific recordings were collected for analyses (2,670 and 722 locations on 21 females and 5 males, respectively).

3.3.1 Second order selection: home ranges within study area

Patterns of habitat preferences did not differ between males and females ($\Delta = 0.71$, $df = 19$, $P = 0.30$). For both sexes, habitat composition within home ranges differed from habitat availability within the study area ($\Delta = 0.40$, $df = 20$, $P < 0.01$). Home ranges of radio-tracked skunks contained more wetlands, rights-of-way, managed nesting areas, and farmsteads and less cropland and woodland than the overall study area (Table 3.1).

3.3.2 Third order selection: locations within home ranges

I first assessed if patterns of habitat selection varied between sexes and among biological seasons. To prevent biases arising from an unbalanced design, I limited this first analysis to animals tracked during all seasons.

Table 3.1. Second order habitat selection (home ranges within study area) by striped skunks ($n = 26$) in Saskatchewan, Canada, 1993-1994. Matrix indicates pair-wise comparisons (i.e., relative selection of habitat in rows compared to habitat in columns) of selectivity coefficients (logratios of percent use over percent availability). Single signs give the tendency and triple signs indicate a significant difference at $\alpha = 0.05$. Selection ranks summarize the comparisons by ranking habitats from the least selected to the most selected. Habitat categories are managed nesting area (MNA), farmstead (FARM), right-of-way (ROW), woodland (WOOD), cropland (CROP), wetland (WET), and miscellaneous habitats (MISC).

	Selection rank	MNA	FARM	ROW	WOOD	CROP	WET	MISC
MNA	5		+	-	+++	+	-	+
FARM	4	-		-	+++	+	-	+
ROW	6	+	+		+++	+	-	+++
WOOD	1	---	---	---		---	---	---
CROP	3	-	-	-	+++		-	+
WET	7	+	+	+	+++	+		+
MISC	2	-	-	---	+++	-	-	

Because few animals were followed during the pre-parturition period, I investigated seasonal differences by comparing the remaining three seasons: parturition/rearing, pre-dispersal, and dispersal. Furthermore, I only considered animals which were tracked for ≥ 1 full 12-h night per season, and for which I obtained ≥ 10 active locations for each season. Because of the high mortality affecting both sexes, and the high rate of dispersal of males captured in the spring (Larivière and Messier 1998), I could only consider six females and three males.

There was no effect of season on patterns of habitat preferences ($\Lambda = 0.52$, $df = 32$, $P = 0.44$), and no interaction between sex and season ($\Lambda = 0.90$, $df = 32$, $P = 0.99$). When I pooled all seasons and considered all males ($n = 5$) and females ($n = 21$) radio-tracked, striped skunks displayed non-random use of available habitat types within their individual home ranges ($\Lambda = 0.14$, $df = 20$, $P < 0.01$), and patterns of preferences did not differ between sexes ($\Lambda = 0.91$, $df = 19$, $P = 0.93$). Overall, striped skunks used wetlands and woodlands more than other habitats, whereas cropland was used significantly less than all other habitats except farmsteads (Table 3.2).

3.3.3 Prey abundance

There was a significant effect of habitat ($F_{5, 11} = 13.6$, $P < 0.01$) and month ($F_{3, 11} = 3.5$, $P = 0.03$) on insect

Table 3.2. Third order habitat selection (locations within home ranges) by striped skunks ($n = 26$) in southcentral Saskatchewan, Canada, 1993-1994. Matrix indicates pair-wise comparisons (i.e., relative preference or avoidance of habitat in rows compared to habitat in columns) of selectivity coefficients (logratios of percent use over percent availability). Single signs give the tendency and triple signs indicate a significant difference at $\alpha = 0.05$. Selection ranks summarize the comparisons by ranking habitats from the least selected to the most selected. Habitat categories are managed nesting area (MNA), farmstead (FARM), right-of-way (ROW), woodland (WOOD), cropland (CROP), wetland (WET), and miscellaneous habitats (MISC).

	Selection rank	MNA	FARM	ROW	WOOD	CROP	WET	MISC
MNA	3		+	-	-	+++	---	-
FARM	2	-		-	-	+	---	-
ROW	4	+	+		-	+++	---	-
WOOD	5	+	+	+		+++	-	-
CROP	1	---	-	---	---		---	---
WET	7	+++	+++	+++	+	+++		+
MISC	6	+	+	+	+	+++	-	

abundance, and no interaction was detected ($F_{15, 11} = 0.77$, $P = 0.70$). Insect abundance increased throughout the summer, being highest in August (Fig. 3.2 A). Overall, insect abundance was highest in farmsteads and rights-of-way, and lowest in cropland. Multiple comparisons indicated significant differences only during August between farmstead and cropland ($P < 0.05$).

There was a significant effect of habitat ($F_{5, 12} = 15.1$, $P < 0.01$) and month ($F_{3, 12} = 13.1$, $P < 0.01$) on small mammal abundance, and no interaction was detected ($F_{15, 12} = 1.07$, $P = 0.42$). Overall, abundance of small mammals increased throughout the summer and peaked in August, and was highest in woodland and farmsteads, and lowest in cropland and managed nesting areas (Fig. 3.2 B). Peromyscus maniculatus, Microtus pennsylvanicus, Clethrionomys gapperi, Zapus hudsonius, and shrews (Sorex cinereus, S. arcticus, S. palustris, and Blarina brevicauda) comprised 48.7%, 19.0%, 14.7%, 3.5%, and 14.1% of all small mammals captured ($n = 1,118$).

3.3.4 Correlation between habitat preferences and prey abundance

There was a significant correlation between ranking of habitat preferences and availability of prey (Spearman rank-order correlation, $r = 0.15$, $n = 26$, $P < 0.01$). An analysis of the relative selectivity of each habitat as a

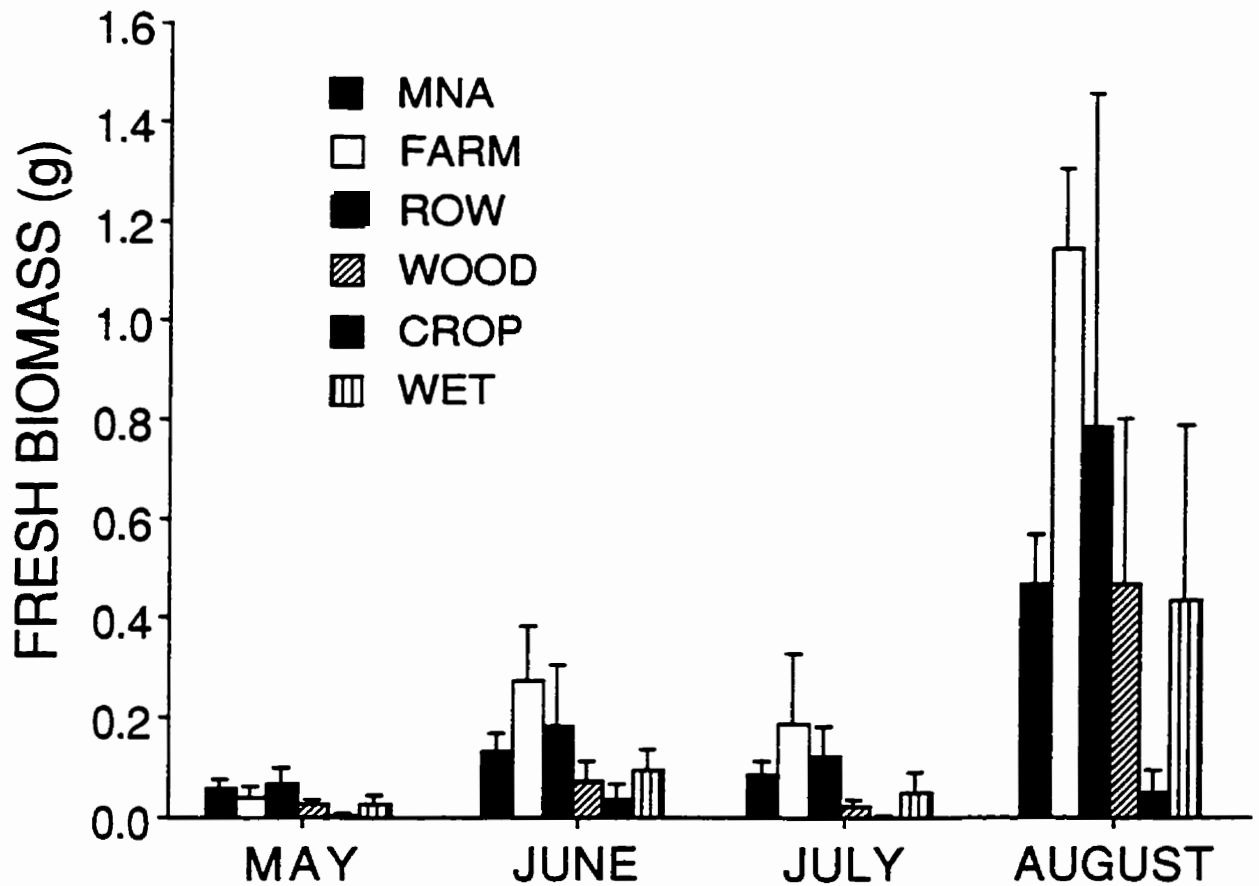


Figure 3.2 A. Mean abundance of insects (g of fresh biomass per 75-m transect) among habitat types in southcentral Saskatchewan, Canada, 1993-1994. Error bars indicate standard error. Habitat categories are managed nesting area (MNA), farmstead (FARM), right-of-way (ROW), woodland (WOOD), cropland (CROP), and wetland (WET).

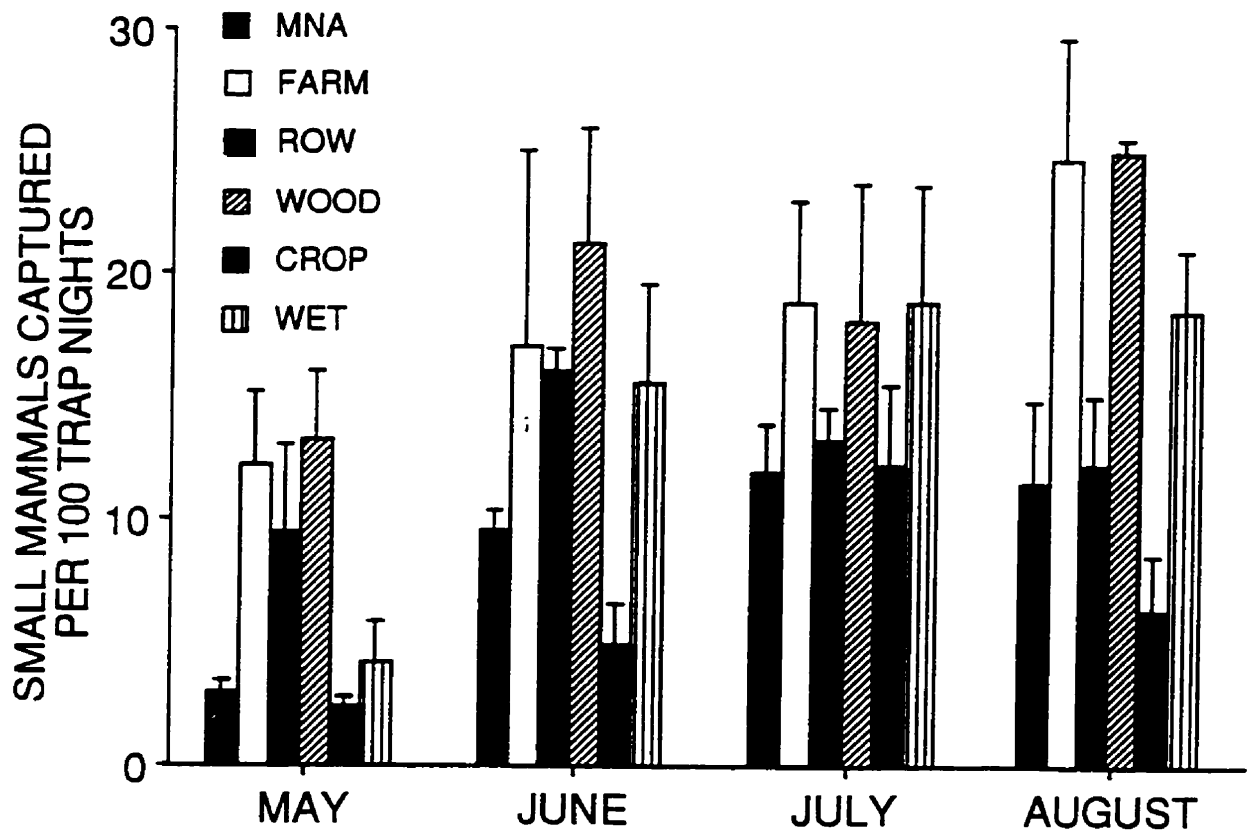


Figure 3.2 B. Mean abundance of small mammals (number captured per 100 trap-nights) among habitat types in southcentral Saskatchewan, Canada, 1993-1994. Error bars indicate standard error. Habitat categories are managed nesting area (MNA), farmstead (FARM), right-of-way (ROW), woodland (WOOD), cropland (CROP), and wetland (WET).

function of its availability of prey showed that differences in ranks were smaller for rights-of-way, woodland, cropland, and managed nesting areas, whereas the greatest disparity of ranks was observed in wetlands and farmsteads (Table 3.3).

3.3.5 Fourth order selection: edge preferences within habitats

There were no effect of sex ($\Lambda = 0.92$, $df = 26$, $P = 0.52$) and habitat ($\Lambda = 0.85$, $df = 52$, $P = 0.61$) on edge use by striped skunks. Similarly, there was no interaction between sex and habitat affecting the relative use of each edge category ($\Lambda = 0.96$, $df = 52$, $P = 0.98$). Thus, I pooled all locations across habitats and again tested for selection of edge categories. When both sexes and all large habitats were considered simultaneously, striped skunks displayed differential use of each edge category ($\Lambda = 0.68$, $df = 20$, $P = 0.05$), with a relative preference decreasing with distance from edge (Table 3.4). Overall, 57%, 19%, 16%, and 8% of foraging locations ($n = 1,354$) of 23 striped skunks were distributed at distances of 0-25, 26-50, 51-100, and >100 m from the nearest edge, respectively (Table 3.4).

3.4 Discussion

Conservation efforts directed at restoring grasslands

Table 3.3. Ranking of prey abundance and habitat preference by male and female skunks in southcentral Saskatchewan, Canada, 1993-1994. Habitat categories are managed nesting area (MNA), farmstead (FARM), right-of-way (ROW), woodland (WOOD), cropland (CROP), and wetland (WET). Habitats are ranked in increasing order of preference, and miscellaneous habitats are excluded from this analysis. Combined prey ranking is obtained by ranking the sum of insect and small mammal ranks for each habitat. Overall use refers to all skunks considered simultaneously using compositional analysis. Mean use (\pm SE) refers to the mean ranking of preferences displayed by individual skunks. The selection index was obtained by calculating the mean differences between the ranks assigned to habitat use and prey availability, where positive values indicate a habitat that is used more than expected based on prey availability.

Habitat	Insect abundance rank	Small mammal abundance rank	Combined prey rank	Mean rank \pm SE (M+F)	Difference (use - prey)
MNA	4	2	2	3.04 \pm 0.20	+ 1.04
FARM	6	5	6	3.92 \pm 0.38	- 2.08
ROW	5	3	4.5	3.65 \pm 0.29	- 0.85
WOOD	2	6	4.5	3.65 \pm 0.36	- 0.85
CROP	1	1	1	1.92 \pm 0.24	+ 0.92
WET	3	4	3	4.81 \pm 0.24	+ 1.81

Table 3.4 Fourth order habitat selection (use of edges) by striped skunks ($n = 23$) in southcentral Saskatchewan, Canada, 1993-1994. Matrix indicates pair-wise comparisons (i.e., relative preference or avoidance of habitat in rows compared to habitat in columns) of selectivity coefficients (logratios of percent use over percent availability). Single signs give the tendency and triple signs indicate a significant difference at $\alpha = 0.05$. Edge categories are 0-25 m, 26-50 m, 51-100 m, and >100 m. All large habitats (managed nesting areas, woodland, and cropland) were considered simultaneously.

Selection		EDGE CATEGORY			
	rank	0-25	26-50	51-100	>100
0-25	1		+	+	+++
26-50	2	-		+	+
51-100	3	-	-		+
>100	4	---	-	-	

for wildlife have been extensive in the last decade. Although they generally have a positive effect on avian species (Kantrud 1993), there has been no assessment of their effects on nest predators. In this study, striped skunks were present in areas where a large proportion of the land is managed as nesting areas (Table 3.1). Importantly, striped skunks did not use these managed nesting areas more than other habitats for foraging (Table 3.2).

At the second order of selection, home ranges of striped skunks contained a higher proportion of managed nesting areas and a lower proportion of woodland and cropland. However, I chose my study areas based on the presence of managed nesting areas hence the pattern found for second order selection may not reflect skunk preferences for managed nesting areas. In addition, fields of managed nesting cover are usually established in areas of high wetland density, and this may explain the preference of wetlands by striped skunks at this order of selection (Table 3.1).

When foraging (third-order selection), habitat selection patterns of most species reflect two constraints: obtaining food and avoiding predation (Lima and Dill 1990). Because of their chemical defence, conspicuous warning colouration, and efficient aposematic behaviour (Larivière and Messier 1996a; Walton and Larivière 1994), striped

skunks have few natural predators. Instead, striped skunk populations are limited by disease and human-related mortality (Sargeant et al. 1982). Furthermore, striped skunks are inactive in winter and the reproductive success of species that undergo dormancy is linked to body condition in late summer and autumn (e.g., Samson and Huot 1995). Thus, obtaining food is an important constraint for striped skunks, and my results suggest that food availability governs habitat selection in striped skunks.

The preference of wetlands by foraging striped skunks is unequivocal (Table 3.2). If food availability explains the overall patterns of habitat selection in striped skunks, this extreme preference of wetlands by foraging skunks becomes enigmatic as wetlands offer neither the highest abundance of insects (Fig. 3.2 A) nor small mammals (Fig. 3.2 B). Furthermore, preference of wetlands is exhibited by most animals with little variation (Table 3.3). Thus, wetlands may provide skunks with water, or with prey items not encountered elsewhere. During this study, striped skunks were frequently observed swimming and wading in water while foraging, and on two occasions, striped skunks foraging in wetlands investigated active muskrat (Ondatra zibethicus) burrows with entrances partially underwater. Thus, it is possible that striped skunks obtain other food items such as overwater bird nests, amphibians, or young muskrats when foraging in wetlands compared to

other habitats. Preference of wetlands by skunks also indirectly supports the hypothesis that in cropland dominated landscapes, wetland margins act as ecological traps for nesting waterfowl (Crabtree et al. 1989; Krasowski and Nudds 1986).

Another habitat type, farmstead, provides the opposite enigma with regard to its use by foraging striped skunks: farmsteads bear the highest abundance of insects, the second highest abundance of small mammals (Fig. 3.1) and yet, they were rarely used by foraging skunks (Table 3.2). Interestingly, female striped skunks make extensive use of farmsteads as maternal denning sites (Chapter 2). Possibly, female skunks may avoid foraging in farmsteads containing their maternal den to maintain high abundance of prey to 1) enhance encounters between juvenile skunks and prey during the pre-dispersal period, and 2) maintain a proximate supply of food during energetically stressful periods (e.g., parturition and early lactation) when activity is restricted to the immediate proximity of the den (Larivière and Messier 1997b). Indirect support for the latter hypothesis may be indicated by the highest use of farmsteads occurring during the parturition/rearing period (S. Larivière and F. Messier, unpubl. data). However, why female skunks do not make more extensive use of farmsteads not used as maternal den sites, or any farmstead during the dispersal period, and why males avoid farmsteads throughout

the summer, remains enigmatic.

The strong avoidance of cropland by foraging skunks (Table 3.2) is not surprising considering that cropland harbours the lowest abundance of insects and small mammals (Fig. 3.1). Aside from corn and sunflowers which are directly used as food by skunks (Verts 1967), small grain or oil crops offer little in terms of food. Furthermore, annual crops offer little structural heterogeneity, harbour a low abundance of both insects and small mammals (Fig. 3.1), and are rarely used by nesting waterfowl (Klett et al. 1988) or songbirds (Hartley 1994).

Managed nesting areas undergo periodic (every 5-10 years) maintenance which may involve haying, burning, tilling and reseeding. Maintenance of nesting habitats is scheduled to prevent an overly high density of perennial grasses which may hinder the movements of freshly hatched ducklings. In addition, maintenance of managed nesting areas prevents the build-up of ground litter, and decreases the abundance of forbs which in turn decrease their use by small mammals (Schwartz and Whitson 1987). Typically, tilling results in lower abundance of small mammals (Hall and Willig 1994) and nesting passerines (Basore et al. 1986; Kantrud and Stewart 1984). The results from this study support the value of periodic burning (Johnson and Temple 1990), or tilling (Choromanski-Norris et al. 1989) as management practices: the lowest abundance of both

insects and small mammals were found in the only two habitats which undergo periodic maintenance, CROP and MNA (Fig. 3.2).

In theory, edge preferences may be predicted by assuming that foraging animals tend to forage near high-quality habitats (Andrén 1995). Thus, an animal located in a low-quality habitat should be closer to the edge of this habitat, simply because of its higher availability of resources (e.g., food). In my study, striped skunks avoided cropland and managed nesting areas. As predicted, striped skunks used edges more than the interior of these habitats during foraging (Table 3.4). Field observations suggested that striped skunks often use field edges when rapidly travelling around wetlands and other dense habitats. However, I do not believe that dense vegetation impairs or reduce skunk movements into habitat interior (e.g., Crabtree et al. 1989). Instead, I believe that skunks focus their foraging activity in and around the vicinity of key habitats (e.g., wetlands). Thus, edge effects observed in predation rates of waterfowl nests in small (<64 ha) managed nesting areas (e.g., Pasitschniak-Arts and Messier 1995) and large (~200 ha) homogenous patches of native prairie (Pasitschniak-Arts and Messier 1996) are likely a consequence of the lack of ecological features such as wetlands (this study) or farmsteads (Chapter 2) attracting skunks into the habitat interior.

For managers interested in mitigating predation on waterfowl nests, habitat management is often preferred to more expensive or controversial techniques such as predator control or exclusion. I have previously suggested that management of den sites may yield a non-destructive avenue of predation abatement (Larivière and Messier 1998; Chapter 2). In addition, my results highlight the importance of wetlands as foraging habitats for striped skunks. Because wetlands are critical to successful waterfowl recruitment, removal of wetlands is obviously not an option. However, large blocks of nesting cover which contained wetlands on their perimeter instead of within, would still provide adequate nesting cover for waterfowl while possibly decreasing the use of their interior by foraging skunks. In addition, large patches of nesting cover are more likely to be avoided by skunks, especially if they contain no biological attraction points such as wetlands and/or farmsteads (Chapter 2). Recent literature reports higher nesting success in large versus small habitat patches for both waterfowl and passerine birds (Arango-Vélez and Kattan 1997; Ball et al. 1995; Gibbs 1991; Kantrud 1993). Thus, the combination of large habitat patches with wetlands on the periphery, in addition to the removal of nearby high-quality maternal denning structures (i.e., buildings), may increase the nesting success of upland nesting waterfowl by decreasing their use by striped skunks.

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4. EFFECTS OF NEST DENSITY AND NEAREST NEIGHBOURS ON THE SURVIVAL OF SIMULATED WATERFOWL NESTS: CAN PREDATORS RECOGNIZE GOOD NESTING PATCHES?

4.1 Introduction

Nest predation is the most important cause of reproductive failure in birds (Ricklefs 1969; Böhning-Gaese et al. 1993). As a consequence, adaptations to counteract predation on nests are numerous (Lack 1968), and include reduction of nest accessibility (Martin 1988, 1995), reduction of clutch size (Julliard et al. 1997), concealment of nest sites (Schieck and Hannon 1993), cryptic colouration of eggs (Götmark 1992), and nest defense (Cresswell 1997). Spacing of nests may also reduce predation by diminishing the foraging efficiency of predators (Tinbergen et al. 1967; Lack 1968). Although the advantages of spacing out nests have been addressed mathematically (Taylor 1976), there is no consensus among ecologists as to whether nest predation is density dependent or independent (Göransson et al. 1975; Andrén 1991; Paton 1994). Furthermore, results from studies linking nest density and nest success are often confounded by habitat variables and nest concealment (reviewed by Clark and Nudds 1991; Niemuth and Boyce 1995).

With expansion of agriculture and subsequent fragmentation of natural grasslands, nesting cover for upland nesting waterfowl has been reduced, leading to the possible concentration of waterfowl nests in smaller

patches (Hill 1984a; Kantrud 1993). Although numerous studies have addressed the effects of density on nest survival in birds (reviewed by Paton 1994; Major and Kendal 1996), few studies have addressed the question for waterfowl (Clark and Nudds 1991). Furthermore, it is unknown whether generalist predators, which prey on nests opportunistically, can recognize and key on high quality patches, thus causing stronger density effects with time.

A possible mechanism for density-dependent nest predation is that upon encounter with a nest, predators exhibit area-restricted searching behaviour (Tinbergen et al. 1967). Thus, the fate of an individual nest becomes linked to the fate of its nearest neighbour (e.g., Hill 1984b; Salonen and Penttinen 1988). The prediction is that at higher densities, nearest neighbour effects should be stronger than at lower densities, since the probability of encountering a second nest is greater.

Herein, I experimentally address the effects of nest density and proximity to neighbours on the survival of simulated nests. I predicted that 1) nest predation should be density-dependent; 2) nearest neighbour effects should be stronger at higher nest densities; and 3) nest destruction should occur faster in late nesting season as a result of predators recognizing high quality patches.

4.2 Materials and methods

4.2.1 Study area

Experiments were conducted in the Prairie Pothole Region of southcentral Saskatchewan (52°45' N, 107°08' W). Small grain (i.e., wheat, barley, oats) and oil crops (mostly canola and flax) occupy 60% of the landscape. Numerous wetlands and stands of trembling aspen occur throughout the area. Topography is gently-rolling, and the land is divided by an extensive network of roads. Managed waterfowl nesting areas are common throughout the area, and consist mostly of dense nesting cover, a mixture of native and tame grasses seeded specifically to attract upland nesting waterfowl. Other characteristics of the Prairie Pothole Region are detailed elsewhere (Greenwood et al. 1995).

In this area, the striped skunk is the principal nest predator (Pasitschniak-Arts and Messier 1995a), but other mammalian predators including red fox (Vulpes vulpes), coyote (Canis latrans), raccoon (Procyon lotor), and North American badgers (Taxidea taxus) are present. Birds such as magpies (Pica pica), and crows (Corvus brachyrhynchos) also occur (Klett et al. 1988, Johnson et al. 1989).

4.2.2 Experimental design

I used a randomized block design where each block ($n = 5$ replicates, hereafter referred to as A-E) consisted of a

quarter section (800 x 800 m) of managed nesting cover. Fields of managed nesting cover were neither cut nor hayed, and were sown primarily with alfalfa, brome, and crested wheatgrass to create prime habitat for nesting waterfowl (Kantrud 1993). All replicates were located in adjacent sections (1.6 x 1.6 km) of land, and all had similar vegetation except replicate E which was comprised solely of alfalfa.

Within each block, three treatment quadrats were positioned to maximize distance between quadrats, leaving >50 m from any habitat edge to prevent possible edge effects (Pasitschniak-Arts and Messier 1995a). Natural densities of waterfowl nests vary between 0.01-5.93 nest/ha on mainland (Higgins 1977; Duncan 1987; Andrén 1991), and current densities seldom exceed 2.5 nests/ha (Duebbert and Lokemoen 1976). For my experiment, I selected densities of 2.5, 10, and 25 nests/ha to compare density effects at current densities (2.5 nests/ha), with extremely high densities (10-25 nests/ha) which could be found in habitat fragments. This broad range of nest densities also facilitated detection of density-dependent predation. Intermediate (10 nests/ha) and high (25 nests/ha) density quadrats were 2 ha (100 x 200 m) in size, whereas low (2.5 nests/ha) density quadrats were increased to 4 ha (200 x 200 m) in size to increase the total number of nests per quadrat.

Within each quadrat, I randomly selected nest locations, with the constraint that no nest could be <5 m from its nearest neighbour; randomizing nest sites prevented predators from systematically destroying nests. Nest locations were marked one week prior to the onset of the experiment with numbered bamboo canes. To prevent predators from cueing on nest markers (e.g., Picozzi 1975), actual position of nest was selected within a 3-m radius of each nest marker, and the direction recorded to facilitate nest visits. Furthermore, I marked with bamboo canes 25 nest locations per ha, regardless of the density of simulated nest deployed in each quadrat. In the high density quadrat, an extra 25 locations per ha were marked. Thus, $\geq 50\%$ of nest markers were not associated with simulated nests. I also standardized the amount of human scent among plots by visiting 25 marked locations/ha during each visit, in each quadrat, although nests were deployed only at selected densities. Finally, I never visited more than 5 marked nest locations from any entry point in the quadrat to prevent creating a continuous scent trail leading to each nest deployed. Rubber gloves were worn at all times during nest deployment and nest visits.

4.2.3 Simulated nests

Simulated waterfowl nests consisted of six chicken eggs deposited in a small (15-cm) depression in the ground,

and covered with dead vegetation. Two drops of commercial duck scent (Robbins Scent Inc., Connellsville, PA 15425) were deposited at each nest visit to simulate the presence of an incubating female. Eggs were dyed with tea to a dull-brown colour to resemble natural duck eggs. Simulated nests were not used to estimate predation rate on natural nests, but instead as a means to quantify spatio-temporal patterns of nest predation in prairie landscapes.

Nests were deployed on May 15 and left in place for 25 days. Because waterfowl often renest following depredation of the first clutch, the experiment was repeated on June 15, randomly alternating the position of each nest within all quadrats. I voluntarily performed temporal pseudoreplication (Hurlbert 1984) by repeating the same treatment at the same quadrats within each replicate. By doing so, I provided a better reflection of natural conditions where better nesting patches often remain more heavily used throughout the nesting season, and this design enabled us to assess whether nest predators recognized high quality nesting patches (Yahner and Mahan 1996).

Nests were visited every 5 days. A nest was considered depredated when ≥ 1 egg was damaged or missing (Sugden and Beyersbergen 1986), and all remaining intact eggs were removed following depredation. Because survival rate of individual nests is not independent from that of other nests within the same quadrat, the quadrats were considered

as the basic sampling unit. Calculations of survival probabilities for each experiment followed Mayfield (1975).

4.2.4 Predator identification

Mammalian predators cannot be identified strictly from nest remains (Larivière and Messier 1997a). Thus, I used thin wire haircatchers (Pasitschniak-Arts and Messier 1995b) positioned above the nest to identify mammalian predators. Because of their size (see Pasitschniak-Arts and Messier 1995b), haircatchers are most effective for medium-sized mammals such as striped skunks, raccoons, red foxes, and coyotes. Nonetheless, their use provided an index of species present in my study area, and permitted comparison of the relative importance of each species among replicates. Hairs were identified using scale patterns (Moore et al. 1974; Adorjan and Kolenosky 1980).

4.2.5 Vegetation measurements

Vegetation measurements were taken during the two-day interval separating the two trials. I compared vegetation characteristics among replicates by sampling the four corners of each quadrat. At each corner, a Robel pole was positioned, and I recorded mean height of vegetation (in cm, estimated by visual obstruction on Robel pole), litter depth (in cm), and percentages of cover and standing vegetation (estimated to the nearest 10%).

4.2.6 Statistical Analyses

Since the survival probability of nests is likely spatially autocorrelated within a quadrat, I maximized the independence of my data by using each quadrat as the basic sampling units (i.e., replicates). Thus, for all density analyses, I considered only one datum for each replicate/density combination.

I first tested for constant survival through time using non-parametric Friedman repeated-measures analysis of variance on ranks. Consequently, effects of density and season on nest survival were tested using repeated-measures analysis of variance to assess main effects and possible interactions between season and density. Differences in the proportion of nests for which the nearest neighbour was successful versus depredated was tested during each nest visit using a 2x2 contingency table and Fisher exact test. Vegetative characteristics were compared among replicates and densities using multivariate analysis of variance (Sokal and Rohlf 1981). For this analysis, Robel pole readings and litter depth were transformed using natural logarithms, whereas percentages of cover and percentage of vertical vegetation were arcsine transformed (Sokal and Rohlf 1981). All statistical procedures were performed using 2-tailed probability levels, and P values ≤ 0.05 were considered significant. Values are reported as mean \pm standard error unless stated otherwise.

4.3 Results

4.3.1 Test for constant survival rate

I hypothesized that nest survival should decline with time due to predators finding high-density patches. I predicted that nest survival would remain constant through time at low density, whereas it would decline with time at high densities. Because I expected an interaction between density and visit (i.e., different effect of time among densities), I considered each density separately in my analyses, and combined both early and late season to increase the power of the test.

Survival rates were constant at low density ($F_r = 6.3$, $n = 8$, $df = 4$, $P = 0.18$), but varied significantly at both medium ($F_r = 12.8$, $n = 6$, $df = 4$, $P = 0.01$) and high densities ($F_r = 25.0$, $n = 9$, $df = 4$, $P < 0.01$; Table 4.1). For all densities, there was a trend for survival to decrease with time (Fig. 4.1). Thus, I weighted daily survival probabilities by using the number of nests present at the beginning of each period as the weighting factor in subsequent analyses.

4.3.2 Nest survival in relation to nest density and season

There was a significant interaction between season and density on the survival of simulated nests ($F_{2,12} = 6.68$, $P = 0.01$). Thus, I examined both effects separately.

In early season (15 May - 13 June), there was no

Table 4.1. Survival rates of simulated waterfowl nests deployed at three different densities in Saskatchewan, Canada, during the 1995 waterfowl breeding season. \bar{n} indicates the initial number of nest deployed in each experimental quadrat. Overall mean and SE include complete rows only.

Season	Density (\bar{n}) (nests/ha)	Replicate	Exposure days				
			5	10	15	20	25
Early Season	2.5 (10 nests)	A	0.98	0.89	0.60	-	-
		B	1.00	0.93	0.70	0.60	-
		C	1.00	0.93	1.00	0.97	0.96
		D	1.00	1.00	0.93	0.89	1.00
		E	1.00	1.00	1.00	1.00	0.98
	10 (20 nests)	A	0.99	0.88	0.78	0.92	1.00
		B	1.00	1.00	0.88	0.94	0.87
		C	0.99	0.99	0.96	1.00	0.96
		D	1.00	0.93	0.87	0.89	0.60
		E	1.00	1.00	0.98	0.99	0.91
	25 (50 nests)	A	0.96	0.88	0.72	0.87	0.60
		B	1.00	0.97	0.94	0.76	0.94
		C	1.00	0.99	0.98	0.95	0.90
		D	1.00	1.00	0.95	0.98	0.94

		E								
Overall mean (\bar{n} = 13)				1.00	1.00	0.95	0.98	0.94		
SE				0.995	0.967	0.919	0.934	0.892		
				0.003	0.123	0.024	0.019	0.037		
Late Season	2.5 (10 nests)	A		1.00	0.83	0.87	1.00	0.87		
		B		0.93	0.93	0.90	0.92	0.87		
		C		0.96	1.00	0.97	0.78	0.60		
		D		0.96	1.00	0.94	0.92	0.87		
		E		0.83	1.00	1.00	1.00	1.00		
	10 (20 nests)	A		0.90	0.89	0.70	0.60	-		
		B		0.93	0.70	0.87	0.60	-		
		C		0.93	0.99	0.79	0.76	0.60		
		D		0.87	0.67	0.60	-	-		
		E		0.87	0.83	0.60	-	-		
25 (50 nests)	A		0.97	0.93	0.69	0.87	0.60			
	B		0.94	0.83	0.73	0.60	-			
	C		0.98	0.96	0.93	0.68	0.92			
	D		0.96	0.98	0.96	0.91	0.84			
	E		0.91	0.94	0.93	0.96	0.60			
Overall mean (\bar{n} = 10)				0.943	0.956	0.898	0.880	0.777		
SE				0.015	0.017	0.030	0.034	0.050		

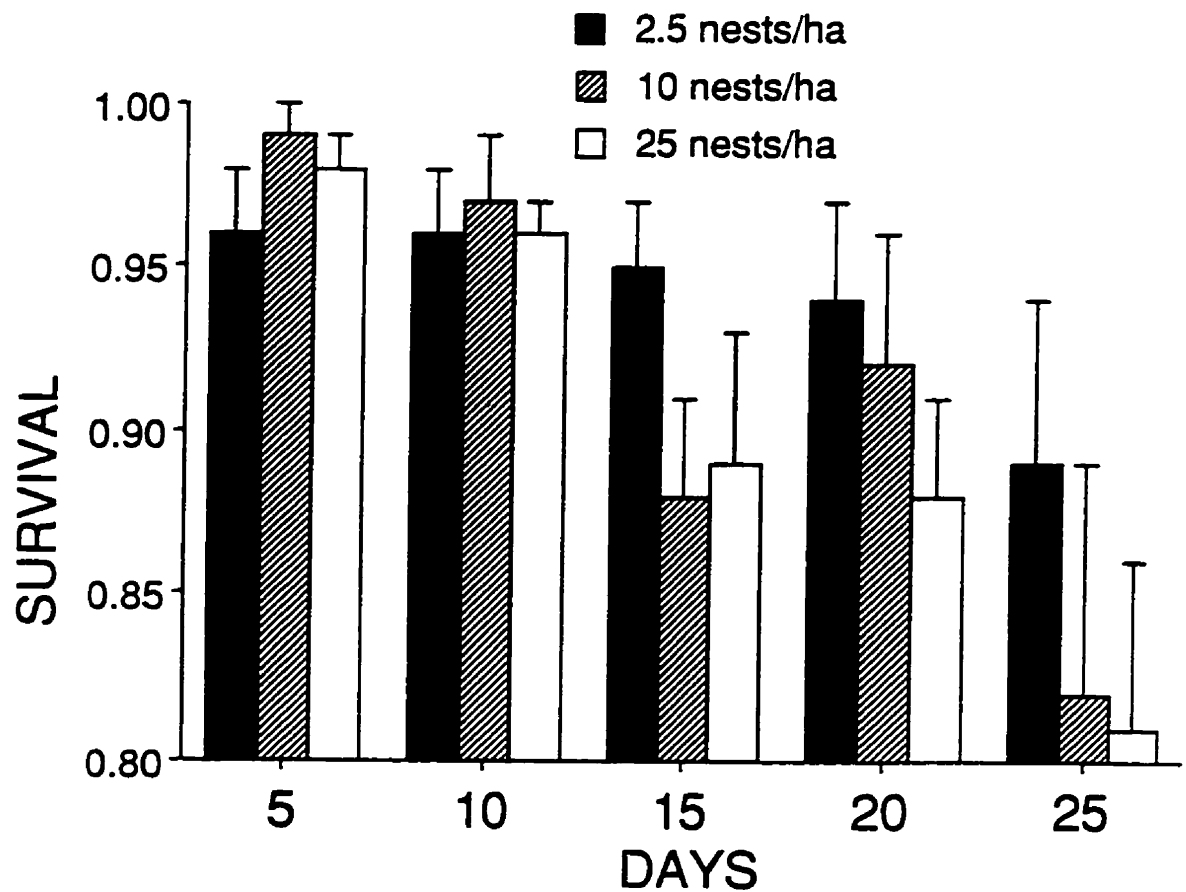


Figure 4.1. Temporal variations in survival (Mayfield estimate) of simulated nests deployed at three experimental densities during the 1995 breeding season of waterfowl in Saskatchewan, Canada. Error bars indicate standard errors.

effect of density on the survival of simulated nests ($F_{2,12} = 0.54$, $P = 0.95$; Table 4.2). Proportion of survivors after 25 days were 36.0%, 29.0%, and 25.2% for the low, medium, and high densities, respectively (Fig. 4.2).

During the late season (15 June - 13 July), density had a significant effect on nest survival ($F_{2,12} = 12.05$, $P < 0.01$). After 25 days, the probability of nest success was 16.0%, 0.0%, and 4.0% at the low, intermediate, and high density, respectively (Fig. 4.2). Similarly, mean daily survival was lowest at the intermediate nest density (10 nests/ha), and highest at the low density (Fig. 4.3).

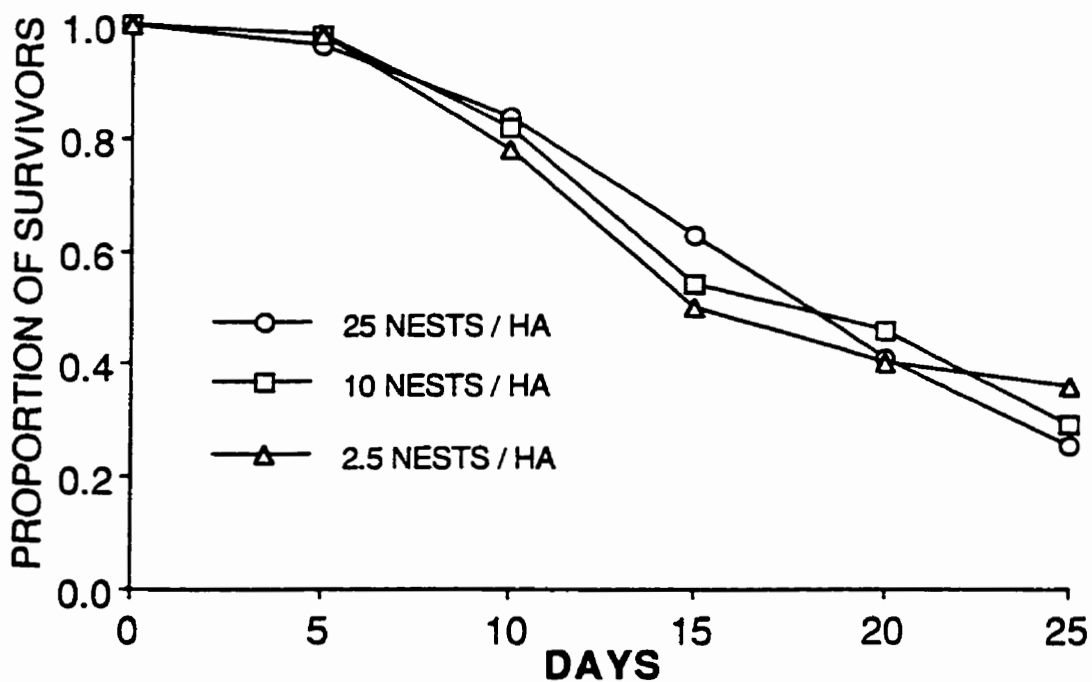
At low nest densities (e.g., 2.5 nests/ha), season (early versus late) did not affect nest survival ($t = 0.43$, $df = 8$, $P = 0.68$). However, nest survival differed significantly between seasons when nests were deployed at intermediate nest densities (i.e., 10 nests/ha; $t = 4.82$, $df = 8$, $P < 0.01$). At high nest densities (i.e., 25 nests/ha), a trend for lower success during the late season was detected, although it was not significant ($t = 1.93$, $df = 8$, $P = 0.09$; Table 4.2).

Interestingly, the mean daily survival was heterogenous among replicates ($F_r = 9.467$, $n = 5$, $df = 4$, $P = 0.05$), hence supporting my experimental block design. Survival of simulated nests was lower in replicate A, and higher in replicate E and C (Table 4.2).

Table 4.2. Effects of density, season, and replicate on the daily survival of simulated nests in Saskatchewan, Canada, during the 1995 waterfowl breeding season. Values indicate the weighted mean for each replicate-season-density combination. Seasons are spring (15 May - 13 June) and summer (15 June - 14 July).

Replicate	Season	Nest density		
		2.5 nests/ha	10 nests/ha	25 nests/ha
A	Spring	0.865	0.908	0.879
	Summer	0.910	0.856	0.883
B	Spring	0.886	0.948	0.934
	Summer	0.919	0.830	0.862
C	Spring	0.972	0.980	0.969
	Summer	0.914	0.890	0.914
D	Spring	0.964	0.913	0.954
	Summer	0.947	0.796	0.942
E	Spring	0.996	0.978	0.976
	Summer	0.934	0.824	0.897
Overall mean \pm SE	Spring	0.936 \pm 0.026	0.946 \pm 0.015	0.942 \pm 0.017
	Summer	0.925 \pm 0.007	0.839 \pm 0.016	0.900 \pm 0.014

A) 15 MAY - 13 JUNE



B) 15 JUNE - 14 JULY

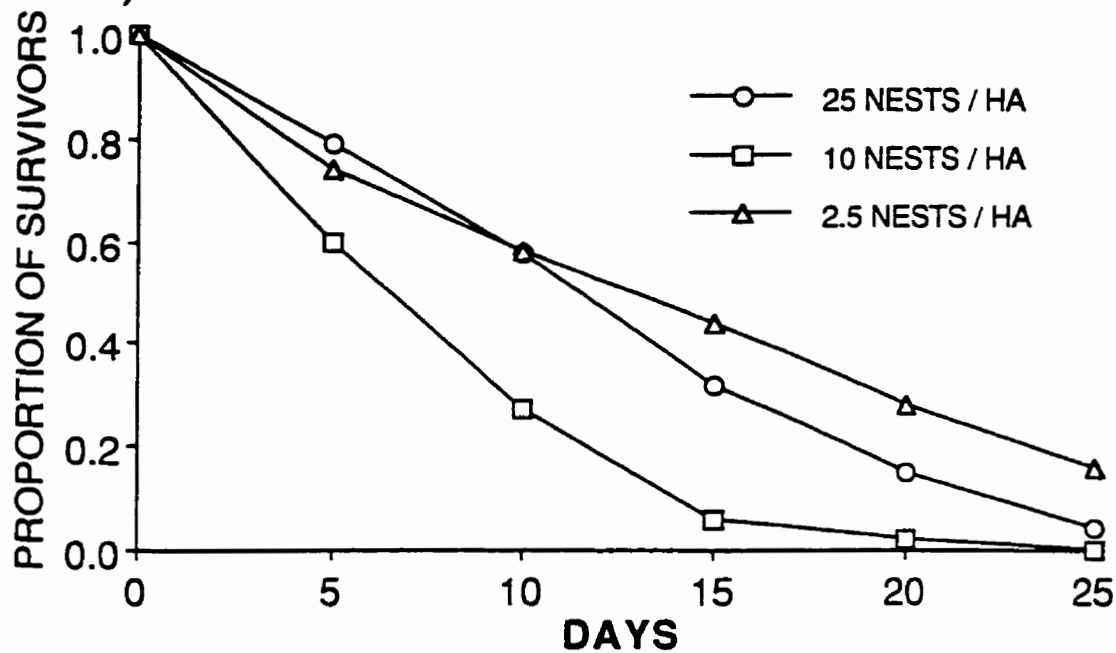


Figure 4.2. Survivorship curves for simulated nests deployed at three experimental densities in the early (May 15 - June 13) and late (June 15 - July 14) breeding season of waterfowl in Saskatchewan, Canada.

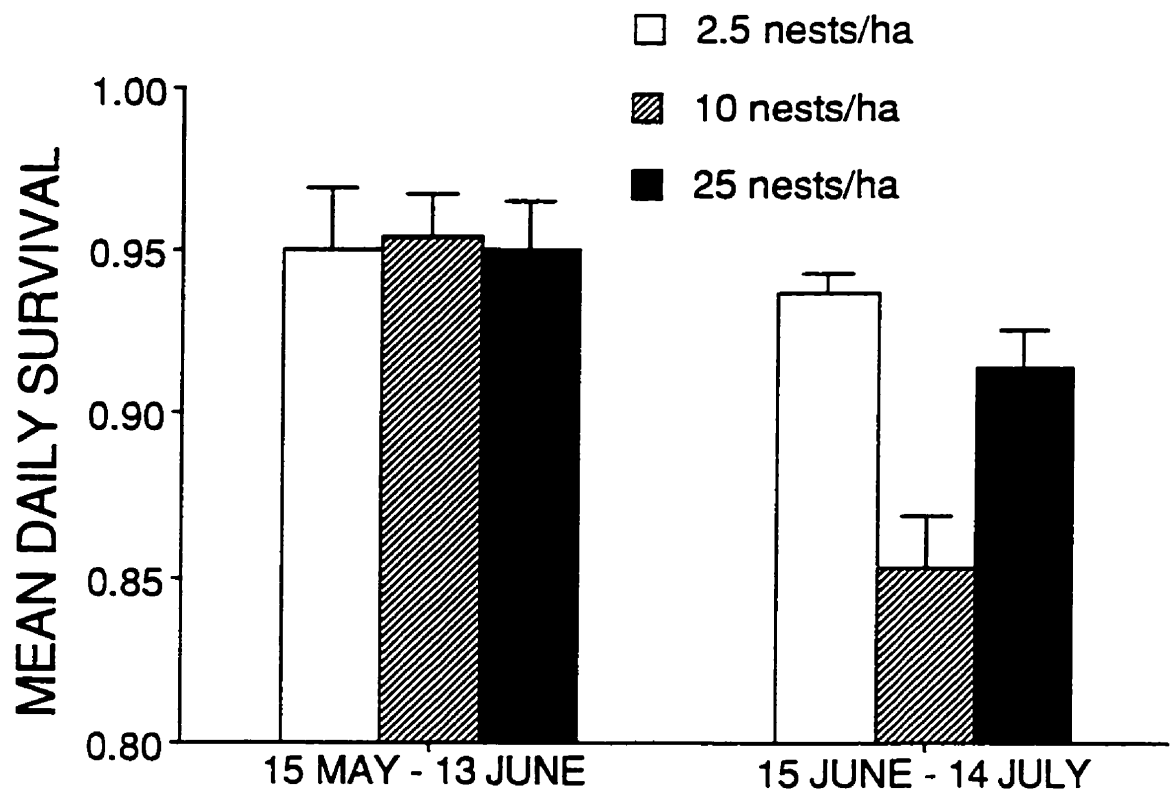


Figure 4.3. Average Mayfield survival of simulated waterfowl nests deployed at three densities in the early (May 15 - June 13) and late (June 15 - July 14) breeding season of waterfowl in Saskatchewan, Canada. Error bars indicate standard errors.

4.3.3 Nearest neighbour effects

I tested the hypothesis that under random patterns of predation, the probability of a neighbouring nest being depredated will be the same as for the entire sample of nests, i.e., there will be no spatial correlation. Nearest neighbour effects were frequent for intermediate and high densities, but rare for low density (Table 4.3). Furthermore, nearest neighbour effects were observed faster and more frequently during the late season compared to the early season (Table 4.3).

Nearest neighbour effects are strongly related to the scale of the area-restricted search behaviour displayed by successful predators. Thus, it is possible that within a given density, the fate of a specific nest is dependent on the distance between this nest and its nearest neighbour. To test this hypothesis, I compared the mean distance to the nearest neighbour between successful and depredated nests after 25 days. Because of high predation rates and low number of survivors (16/400) in the late season, I only performed this analysis for the early season.

Distance to the nearest neighbour did not differ between successful and unsuccessful nests ($F_{1,394} = 0.1$, $P = 0.82$) but differed among nest densities ($F_{2,394} = 184$, $P < 0.01$), and there was no interaction between density and nest fate ($F_{2,394} = 2.2$, $P = 0.11$). Distance between nearest neighbours averaged 38 ± 18 m, 18 ± 10 m, and 11 ± 6 m in

Table 4.3. Probability values of the Chi-square distribution for possible nearest neighbour effects among simulated waterfowl nests deployed at three different densities during the 1995 waterfowl breeding season in Saskatchewan, Canada. n indicates the initial number of nests deployed at each density within each season. * indicate significant values at $\alpha = 0.05$, and ** significant values at $\alpha = 0.01$. Values indicate the ratio of observed/expected for each successful-successful (S-S) and hit-hit (H-H) proportion. Values > 1 indicate higher than expected proportions, indicating that fate of a nest is linked to the fate of its nearest neighbour.

Density (<u>n</u>) (nests/ha)	5 days		10 days		15 days		20 days		25 days	
	S-S	H-H	S-S	H-H	S-S	H-H	S-S	H-H	S-S	H-H
EARLY SEASON										
2.5 (50)	1.00	0.00	1.01	1.05	1.37	2.19**	1.08	3.00	0.99	0.00
10 (100)	1.00	0.00	1.07	2.58**	1.11	1.46 *	1.05	2.79	1.25	1.65*
25 (250)	1.00	3.33	1.05	3.01**	1.11	2.39**	1.26	1.84**	1.18	1.55**
LATE SEASON										
2.5 (50)	1.04	1.30	1.09	1.85	0.86	0.00	1.01	1.03	0.88	0.78
10 (100)	1.19	1.44**	1.73	1.48**	2.17	1.06	-	-	-	-
25 (250)	1.08	2.43**	1.10	1.84**	1.27	1.53**	1.35	1.30**	1.38	1.06

the low, intermediate, and high densities, respectively (Fig. 4.4).

4.3.4 Vegetative characteristics

Vegetative characteristics did not differ among experimental quadrats of various nest density ($\Delta = 0.83$, $df = 8$, $P = 0.45$) and there was no interaction between density and replicate ($\Delta = 0.42$, $df = 32$, $P = 0.15$). However, vegetation characteristics varied among replicates ($\Delta = 0.15$, $df = 16$, $P < 0.01$). Of the four variables examined, mean vegetation height and percentage of vertical cover varied significantly among replicates.

Because replicates differed in vegetative characteristics, I examined the relationships between vegetation and nest success by correlating the survival of simulated nests (using Mayfield's average after 25 days) with mean vegetation height and percentage of vertical cover using Pearson's product-moment correlation (Sokal and Rohlf, 1981). During the early season, there was no correlation between daily nest success and mean vegetation height ($r = -0.42$, $P = 0.48$) or percentage of vertical cover ($r = -0.62$, $P = 0.26$). Similarly, no significant relationships were found during the late season between daily nest success and mean vegetation height ($r = -0.43$, $P = 0.46$) and percentage of vertical cover ($r = -0.26$, $P = 0.67$).

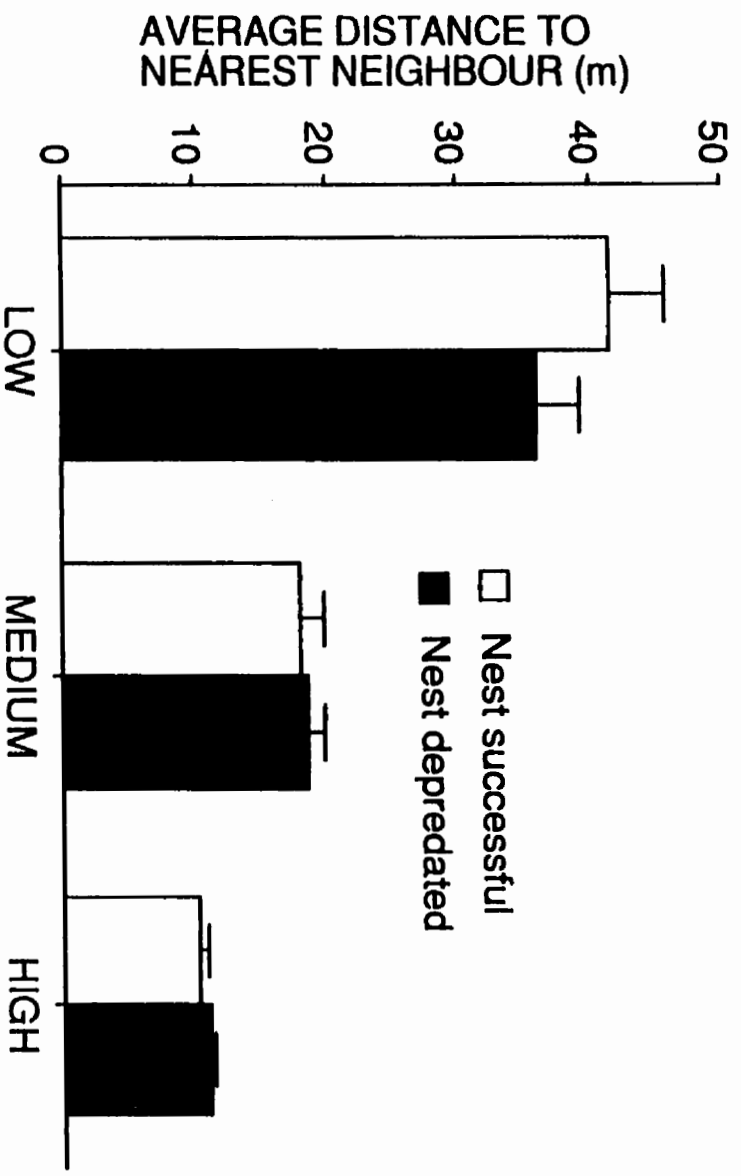


Figure 4.4. Variations in the distance of individual nests to their nearest neighbour in relation to their fate for three experimental densities of simulated nests deployed during the 1995 breeding season of waterfowl in Saskatchewan, Canada. Densities are indicated as low (2.5 nests/ha), medium (10 nests/ha), and high (25 nests/ha). Error bars indicate standard errors.

4.3.5 Predator community

A total of 290 of 400 and 382 of 400 nests was depredated during the early and late trials, respectively, and I collected hair samples at 33% of all depredated nests ($n = 672$). Of those, 83.5% of hair samples collected could be identified to species using scale imprints. Hairs not identified were either not complete, or consisted of underfur which did not allow specific identification. Among identified hair samples ($n = 187$), hairs of striped skunk were most often collected (66.9%), followed by red fox (17.1%), coyote (14.4%), and raccoon (1.6%).

Considering that vegetative characteristics differed among experimental replicates, I examined whether the relative importance of the three main predator species (skunk, fox, coyote) also varied among replicates. Because of the low number of hair samples collected in replicate E ($n = 5$ identified samples), I did not include this replicate in the analysis. Nonetheless, relative importance of each predator species was not homogeneous among replicates A-D ($\chi^2 = 26.7$, $df = 6$, $P < 0.01$). Striped skunks were predominant in all replicates, but their importance was maximum in replicate A (92.6%), whereas the importance of red fox was highest in replicate B (32.6%). Interestingly, all samples ($n = 5$) collected in replicate E were coyote hairs (Fig. 4.5).

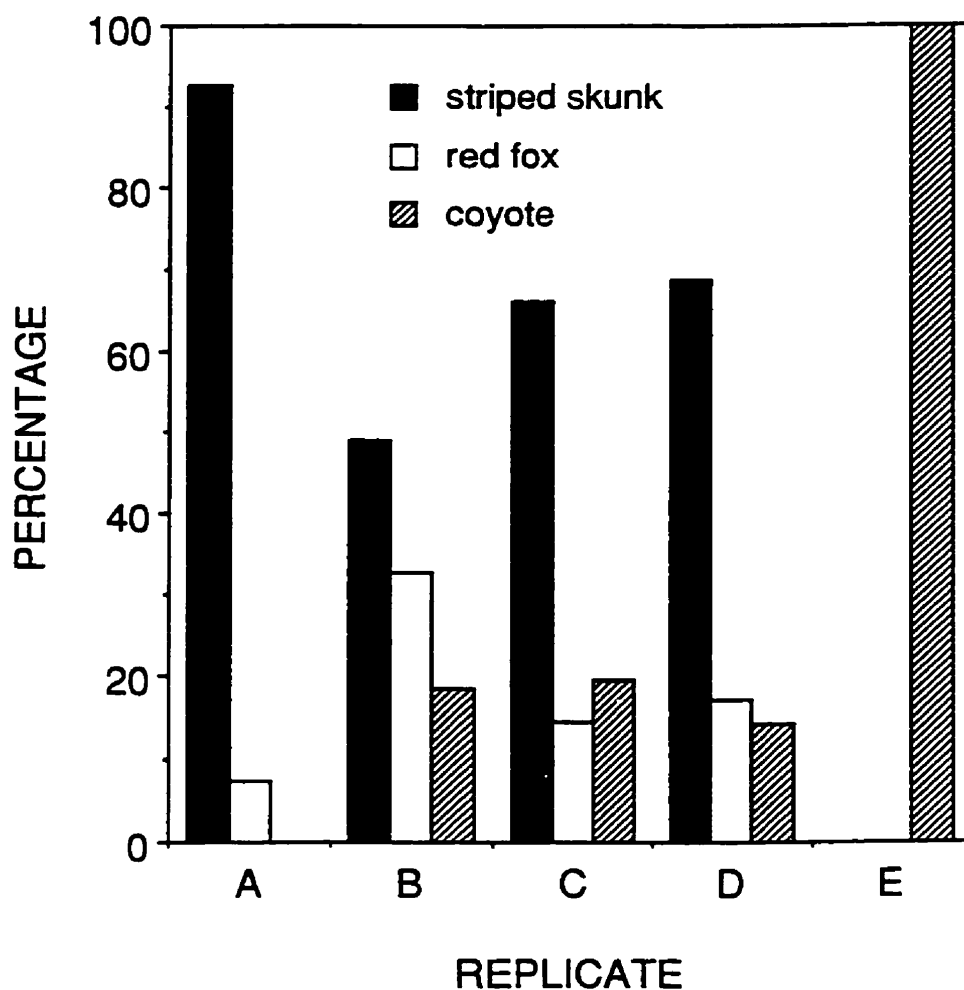


Figure 4.5. Relative importance of three main mammalian predators (striped skunk, red fox, and coyote) in five replicates where simulated waterfowl nests were deployed during the breeding season of waterfowl in Saskatchewan, Canada. Values indicate proportion of hair samples collected in each replicate.

4.4 Discussion

Density-dependent predation affects numerous mammals and birds (Fretwell 1972; Andersson and Wiklund 1978; Galbraith 1988; Hoi and Winkler 1994). Consequently, spacing out as a defense against predation is a common defense strategy for mammals (e.g., Bergerud and Page 1987) and nesting birds (Lack 1968; Major et al. 1994; but see Andrén 1991). This may explain why nesting success of ground-nesting birds increases with patch size (Paton 1994; Ball et al. 1995), especially since birds nesting in larger habitat patches nest at lower densities than birds nesting in smaller patches (e.g., Møller 1987). However, birds nesting in landscapes highly fragmented by agriculture may be forced to nest at higher densities compared to non-fragmented landscapes, simply because of the low availability of suitable nesting habitats. Consequently, nest predators may be exposed to ephemeral patches of abnormally high density, and opportunistic predators may learn to recognize and utilize such resources in response to their high profitability. Thus, density-dependent predation may result, and remaining patches of nesting habitat may become ecological traps for nesting birds.

In this study, density effects did not occur during the early nesting season (mid-May to mid-June), even across treatments with a ten-fold difference in nest density (2.5-25 nests/ha). However, when the experiment was repeated

(mid-June to mid-July), nest success was highest at low nest densities, decreased at densities of 10 nests/ha, and increased again at densities of 25 nests/ha. Furthermore, the same trend was observed in all replicates, strongly suggesting an underlying ecological process. In populations of cryptic nesting birds which do not perform nest defense, nesting success typically decreases with density of nests (e.g., Hoi and Winkler 1994). However, the type of response may be linear only at lower densities (e.g. Fig 44 in Fretwell 1972), then may reach a plateau (e.g. Fig. 45 in Fretwell 1972) or even decrease as nests become extremely common, possibly through satiation of the predators. This may have been the case in my study as nests deployed at high density (25 nests/ha) had slightly higher survival than nests deployed at intermediate densities (10 nests/ha). Further experiments, especially at densities between 2.5-25 nests/ha, are needed before the relationship between density and nesting success of waterfowl can be fully clarified.

A possible mechanism of density-dependent nest predation is that upon encounter with a nest, predators exhibit area-restricted searching behaviour (Tinbergen et al. 1967). If this occurs, then the fate of an individual nest becomes dependent of the fate of its nearest neighbour (e.g., Hill 1984b; Salonen and Penttinen 1988). My results support this hypothesis (Table 4.3). Interestingly, nearest

neighbour effects were observed in the early trial although this did not lead to overall density effects. This time lag in the identification of higher quality patches by nest predators suggests that although mammalian predators depredate nests opportunistically (e.g., Larivière and Messier 1997a), they may take advantage of chance encounters by consequently exhibiting area-restricted searching. However, it is not until the patch is recognized as profitable that predators increase patch use which in turn leads to density-dependent predation (Yahner and Mahan 1996).

Density and nearest neighbour effects in nest predation depend on the type of predators involved, and also on the range of densities or distances involved (Tuda 1993; Hogstad 1995). For example, increasing nest spacing from 10 m to 25 m may not make a difference when highly abundant rats (Rattus sp.) are the main predator, especially if their density is uniform throughout the habitat (Major 1991). However, increasing inter-nest distance may improve nest survival when the main predators exhibit small-scale area-restricted searching (Hill 1984b). In my study, the striped skunk was the most important nest predator, and inter-nest distance did not differ between successful and depredated nests (see also Andrén 1991). In striped skunks, repeated encounters with simulated nests leads to the formation of olfactory search images (Nams

1991). In turn, search images increase the detectability of nests from an initial 3 m up to 25 m (Nams 1997). Within the range of inter-nest distances (11-38 m), only nests deployed at the lower density (average inter-nest distance 38 m) were likely safe from detection by habituated striped skunks. This likely explains the lack of nearest neighbour effects for nests deployed at lower densities (Table 4.3). Alternatively, once a nest is depredated, it becomes more visible to other predators and scavengers which may increase their activity around the nest sites, and thus come in contact with neighbouring nests (Wada 1994). Ultimately, the presence or lack of nearest-neighbour effects will depend on the scales of area-restricted search behaviour exhibited by predators involved, and further investigations of this behaviour are needed before the ecological significance of nearest neighbour effects is fully understood.

The effect of vegetation characteristics on the nesting success of ground nesting birds is unclear (Clark and Nudds 1991) and typically depends on the predator community. For example, shorter vegetation may lead to higher predation rates when the main predators are birds (Dwernychuk and Boag 1972; Hill 1984b). Alternatively, denser cover may impede movements of smaller predators (Crabtree et al. 1989). In my study, not all replicates were similar in mean vegetation height and percent of

vertical cover. However, no relationship existed between those vegetation variables and nesting success and thus, my simultaneous considerations of all replicates was justified. Nonetheless, a relationship existed between vegetation characteristics and the use of each replicate by various nest predators. For example, replicate E had the lowest predation rates (although the same trend for density effects) and the vegetative composition of the plot differed from other replicates by being comprised strictly of alfalfa compared to the mixture of brome grass, crested wheatgrass, and alfalfa present in other replicates. Fields comprised entirely of dense and uncut alfalfa become extremely thick, and may impede skunk movements (Crabtree et al. 1989). Indirect evidence of avoidance by skunks of this replicate was obtained by performing over 2,668 h of radio-tracking on 35 striped skunks during this study, yet I never observed a radio-collared skunk use or even enter replicate E. In addition, no skunk hairs were collected at haircatchers and all samples collected on this replicate were coyote hairs. I suspect that dense alfalfa may increase nest success by reducing use of nesting patches by striped skunks. Finally, the presence of coyotes on replicate E may have decreased use of this field by red foxes (Sovada et al. 1995).

In this study, significant differences in nest survival and vegetative characteristics were observed among

replicates. The variation among fields strongly supports my blocking design where all treatments were replicated within each field. Furthermore, the spatial dependence of nest observed within quadrats provide empirical evidence that the fate of a simulated nest is not independent of other nests in the quadrat or transect, and that instead, the experimental quadrat should be used as the basic unit (i.e., replicate) for analyses.

Replicate A suffered the highest predation, and survival rates were consistently lower than in other replicates (Table 4.2). Higher predation of nests in replicate A may have been related to their proximity to predator dens, mainly the maternal dens of striped skunks (see Larivière and Messier 1998b). During this experiment, three of seven radio-tracked female skunks had their maternal den located within 50 m of replicate A. Furthermore, one female relocated her maternal den inside one of the experimental quadrats in replicate A following initiation of the late season experiment. Female striped skunks display den site fidelity throughout the waterfowl nesting season (Larivière and Messier 1997b), and all foraging activity occurs within small home ranges (ca. 4 km²; Larivière and Messier 1998a). Thus, the location of the den site can greatly influence the survival of nearby waterfowl nests (see also Shields and Parnell 1986; Sullivan and Dinsmore 1990).

My findings must be interpreted with caution as they are based on the use of simulated nests. Locations chosen by humans for simulated nests may not mimic sites chosen by nesting waterfowl (e.g., Guyn and Clark 1997; Butler and Rotella 1998). Furthermore, actual predation rates of simulated nests may be lower than those experience by natural nests, especially because of lack of the olfactory cues associated with the nesting material, and lack of activity at nest site by the hen. Nonetheless, any bias linked to the use of simulated nests were consistent across treatments and replicates, and I believe the patterns observed are reliable.

Predation on nests is not a new phenomenon in evolution, and the current high rates of nest predation are likely a consequence of the response of predators to increased habitat fragmentation. For example, if fragmentation of natural grasslands reduces the availability of nesting cover and therefore concentrates bird nests in smaller patches, then these habitats may become profitable for nest predators which, albeit being generalists, may take advantage of ephemeral or local peaks in nest abundance. Thus, populations of nesting birds may suffer from density-dependent nest predation. In my study, I have demonstrated that predators can indeed recognize high-quality patches, but that some time is needed before predators concentrate their foraging activity within those

patches. Then, density effects occur. However, at current densities (typically <2.5 nests/ha), natural duck nests likely do not suffer from density-dependent predation (Duebbert and Lokemoen 1976), and nest predation by medium-sized mammals remains opportunistic (Vickery et al. 1992; Larivière and Messier 1997). Instead, current high rates of predation on waterfowl nests may be the result of changes in predator communities due to landscape changes (Nour et al. 1993), as well as modification of the foraging strategies of predators in fragmented habitats.

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5. GENERAL DISCUSSION

5.1 Waterfowl nest predation: a synthesis

Predation on nests is a major force affecting the evolution of nesting strategies in birds because it directly affects the reproductive success of individuals (Ricklefs 1969; Böhning-Gaese et al. 1993). Consequently, numerous strategies have evolved to counteract predation on nests (Lack 1968). The relatively recent fragmentation of North American grasslands, a critical nesting habitat for waterfowl, may provide a new evolutionary challenge for North American waterfowl (Báldi 1996).

Proximately, the effects of habitat fragmentation on waterfowl are strongly linked to the response of nest predators to fragmentation (see Huhta 1995). Increased heterogeneity of habitats may allow more species of predators to coexist, or may affect the foraging behaviour of those species. Either scenario may be responsible for the current high rates of predation for waterfowl nests. Although nest predators usually depredate waterfowl nests opportunistically, fragmentation may have resulted in the spatial concentration of bird nests, possibly closer to habitat edges, within specific habitats, or at higher density within smaller nesting patches. In any case, many of the initial adaptations to counteract predation such as nesting away from water, in large habitat patches, or

nesting at low density, may no longer be effective. Hence, habitat fragmentation may lead to high levels of nest predation by opportunistic predators.

As a response to habitat heterogeneity, striped skunks in the Thickwood Hills of Saskatchewan exhibited habitat preferences for the locations of the maternal dens. Farmsteads, which represented only a small fraction (<5 %) of the available habitats, were chosen for ca. 40% of all maternal dens used by female striped skunks (Chapter 2). Alternatively, cropland, managed nesting areas, and woodland were avoided for maternal dens. Because the activity of females is restricted to the vicinity (i.e., within 1 km; Larivière and Messier 1998) of the maternal den throughout the breeding season of waterfowl (Larivière and Messier 1997a), the location of maternal dens had a significant impact on the distribution of foraging activity (Larivière and Messier 1998). Consequently, the locations of maternal dens in proximity of good nesting habitats is predicted to decrease waterfowl nesting success (e.g., Shields and Parnell 1986; Sullivan and Dinsmore 1990), simply because of the limitations imposed by the presence of a dependent litter in the maternal den (Chapter 2).

When foraging, striped skunks used primarily wetlands and woodlands, and again strongly avoided cropland (Chapter 3). Patterns of habitat selection displayed by striped skunks were linked to the availability of insects and small

mammals, although the availability of water and other food sources may have contributed to the high use of wetlands (Chapter 3). Fields of managed nesting areas harbour relatively low abundance of either prey group compared to the more "pristine" habitats such as wetlands and woodland (Chapter 3). Furthermore, in large patches of managed nesting areas, woodland, and cropland, striped skunks use habitat edges more than the habitat interior. Finally, although striped skunks depredate waterfowl nest opportunistically at current densities (<2.5 nests/ha; Larivière and Messier 1997b), patches with high nest densities (e.g., 10-25 nests/ha) are recognized by striped skunks by keying on these patches while foraging, hence causing density-dependent predation (Chapter 4). Interactions between vegetative characteristics and nest survival suggested that fields of managed nesting areas that are comprised entirely of dense alfalfa may experience higher nest survival, possibly by impairing the movements of striped skunks (Chapter 4).

5.2 Management implications

Mitigation of nest predation is not an easy task in wildlife management. Most techniques applied so far (e.g., nesting structures, predator removal, etc.) are only efficient at small spatial and temporal scales. Furthermore, many of these management efforts concentrate

on the proximate cause of waterfowl decline (i.e., predation on nests), and ignore the ultimate cause (i.e., habitat changes).

Habitat alteration and fragmentation is almost inevitable as human populations on Earth continue to increase. However, natural areas still remain, and their importance for wildlife is critical. Therefore, preservation of remaining natural habitats, as well as restoration of critical habitats such as grasslands and wetlands, may provide multi-purpose conservations tool which may benefit multiple species and taxa (Hall and Willig 1994; Hartley 1994; Johnson and Schwartz 1993; Kantrud 1993).

Findings from my research have clearly shown that in a sea of cropland, striped skunks focus their denning and foraging activities on the remaining islands of pristine habitats where insects and small mammals are most abundant (Chapter 2 and 3). Interestingly, managed nesting areas were relatively poor in prey abundance (Chapter 3), and were practically never used for foraging (Chapter 3), or as locations for maternal dens (Chapter 2). Furthermore, the edge of such fields were used more intensively than the interior (Chapter 3).

In conclusion, results from this study add support to the growing body of literature which indicates that nest success of birds may be higher in large versus small

patches (e.g., Ball et al. 1995), and higher in the habitat interior as compared to the proximity of edges (Pasitschniak-Arts and Messier 1995). Large patches of uniform cover, without any inclusions of wetlands or farmsteads, are likely to experience lower use by striped skunks, and possibly higher nest success. Finally, large patches would allow waterfowl to nest at lower density, thus preventing any density-dependent predation.

This study is a small but important step in understanding the ecological consequences of habitat fragmentation on wildlife populations. However, numerous questions remain unanswered. Firstly, the striped skunk is only one of the many mammalian predators of duck nests, and their importance as nest predators varies: in some areas, predators such as red foxes and coyotes may play a bigger role as nest predators (Johnson et al. 1989; Klett et al. 1988). Interestingly, although some of these carnivores have been intensively studied (e.g., red fox; Larivière and Pasitschiak-Arts 1996), little has been done with regards to their response to habitat heterogeneity created by fragmentation. Furthermore, predation on nests is highly variable among areas where different communities of predators exist, yet little information is available on the interactions of different predators on nesting areas (e.g., Sovada et al. 1995). Much work is still needed before the ecological phenomenon of predation on nests is fully

understood. Understanding predators, even if it means species-specific approach, remains critical because every proximate biological factor affecting the fate of bird nests depends first and foremost on the species of predator involved.

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APPENDIX A

THE INFLUENCE OF CLOSE-RANGE RADIO-TRACKING ON THE BEHAVIOUR OF FREE-RANGING STRIPED SKUNKS

Abstract

I assessed the influence of close-range radio-tracking on the behaviour of striped skunks (Mephitis mephitis) in southcentral Saskatchewan. Thirty-five skunks were radio-tracked for 1,873 h from April through August, 1993-1994. Most locations (87%) were performed at a distance >10 m from radio-tracked skunks, whereas 46% were at distances >20 m. Distance travelled between consecutive 15-min locations was not influenced by human disturbance ($P = 0.67$), or by distance from human observer ($P = 0.09$). Skunks did not seek taller or shorter cover following disturbance ($P = 0.21$) or among observation types ($P = 0.57$). However, disturbed skunks remained in the same habitat more than undisturbed skunks ($P = 0.03$). I recommend that locations immediately following observer-induced disturbances be excluded in the analysis of space-use patterns of this species. I nonetheless consider close range radio-tracking a better technique than remote triangulation, especially for disturbance-tolerant species in fine-grained environments.

A.1 Introduction

Conventional triangulation methods using radio-telemetry carry an error related to the imprecision of the triangulation system (Nams 1989; Schmutz and White 1990; Zimmerman and Powell 1995). Although this error can be evaluated (Samuel and Kenow 1992), it can limit inferences about habitat selection (White and Garrott 1986). In fine-grained environments, locational error may also preclude precise assessment of habitat type (Nams 1989), and this error may not be acceptable if the animal makes short movements as compared to the size of the error polygon (Schmutz and White 1990; White and Garrott 1986). Although precise telemetry systems are available (e.g., null-peak systems), fixes must be obtained in close proximity to the study animal to limit measurement error (White 1985), and loss of data may occur when animals move out-of-range of fixed telemetry systems. This has led to the development of ways to mitigate errors associated with radio-locations (Anderson-Sprecher 1994).

Direct observation is the most accurate way of locating an animal, and is limited only by the ability of the observer to locate the animal's position on a map (White and Garrott 1990:42). However, data collected through observation is useful only if the behaviour of the animal is not affected by the presence of the observer (Martin and Bateson 1989:17). Following a moving animal on

foot, aided by the signal of a radio-collar, has been used to obtain precise locations for a wide variety of medium-sized mammals (Erinaceus europaeus, Doncaster 1993; Herpestes ichneumon, Palomares and Delibes 1993; Mephitis mephitis, Crabtree and Broome 1985; Mustela putorius, Lodé 1994; Paradoxurus hermaphroditus, Joshi et al. 1995; Potos flavus, Julien-Laferrière 1993; Vulpes cana, Geffen and Macdonald 1992). Most studies involving direct observation did not mention possible biases created by the presence of an observer. Occasionally, semi-tame (Nams 1991) or human habituated animals (Henry 1986; Watanuki and Nakayama 1993) have been used, and ways to minimize disturbance suggested (Geffen and Macdonald 1992). However, quantitative testing of the effects of human disturbance on movements is still lacking for most species. In this paper, I assess the impact of close range radio-tracking on three components of the space-use patterns of striped skunks: movements, cover use, and habitat use.

A.2 Study area and methods

This study was conducted in the parkland region of southcentral Saskatchewan (52°45' N, 107°08' W). Small grain (i.e., wheat, barley, oats) and oil crops (mostly canola and flax) occupy 60% of the landscape, and numerous wetlands and stands of trembling aspen occur throughout the area. Topography is gently rolling, and the land is divided

by an extensive network of roads. General characteristics of the Prairie Pothole Region are detailed elsewhere (Greenwood et al. 1995).

From April to August, 1993-1994, striped skunks were captured and anesthetized using halothane and Telazol® (Larivière and Messier 1996a, 1996b). All individuals were equipped with a 5-sec delay motion sensitive radio-collar (150-152 Mhz, Telonics Inc., Mesa, Arizona, USA) to monitor activity during tracking (Larivière and Messier 1997b). Skunks were released at the site of capture.

Focal animals were radio-tracked in blocks of 12 hours, from 1800 to 0600. Animals were located by a single observer, on foot, every 15 min, preferably by sight, but also by sound, and short-range (<50 m) triangulation. Throughout tracking, observers remained downwind, silent, and as far as possible from the animal while still being able to locate the skunk accurately. Furthermore, observers only moved when radio-collared animals moved, as indicated by the motion sensor. No headphones were used with the telemetry receiving unit to facilitate awareness of auditive warnings by skunks (Larivière and Messier 1996c) and to facilitate locating skunks by sound. To minimize auditory disturbance, receiver gain was kept to a minimum, and receiver was used only when the skunk was out of sight. Light-amplifying, night-vision goggles (AN-PVS 5, Bill's Electronics Ltd., Mildmay, Ontario) facilitated visual

observations at night.

At each location, distance between skunk and observer was paced (1 step = 1 m), following departure of the skunk, and classified in one of four categories: 0-5, 6-10, 11-15, and 15-50 m. Observations >50 m were excluded from analysis as they were often associated with rapid and extensive movements by the skunk. At each location, mean height of vegetation was classified as 0-0.5, 0.5-1, and >1 m. Habitat type was recorded and then classified in six cover categories defined a priori according to overall thickness and height of vegetation: 1) fallow fields, 2) pastures, 3) farmsteads, fencelines and rights-of-way, 4) cropland, 5) hayland, and 6) woodland and wetlands. Universal Transverse Mercator coordinates were obtained from the exact location of the skunk following its departure from the area using a portable Global Positioning System (Ensign GPS, Trimble Navigation, Cansel Survey Equipment, Burnaby, British Columbia). Distances between consecutive 15-min locations were determined using UTM coordinates incorporated in the software package Ranges IV (Kenward 1990).

Striped skunks exhibit aposematic behaviour, and defensive postures are obvious (Larivière and Messier 1996c). Time and distance between skunk and observer during observer-induced disturbances were recorded throughout tracking. A disturbance was defined as an encounter between a human observer and a skunk which triggered defensive

behaviours by the skunk (Larivière and Messier 1996c). Each location was classified as: 1) no obvious disturbance occurred within last 15 min, or 2) at least one obvious disturbance occurred within the last 15 min.

I investigated the effect of disturbance on skunk movements using a Wilcoxon signed-rank test. Then, I investigated how distance from human observer influences skunk movements using a Friedman two-way analysis of variance on ranks. Chi-square tests of homogeneity were used to assess the influence of vegetation height and cover on the probability of disturbance, type of observation, and probability that the skunk moved to a different habitat following disturbance. Two-tailed probability levels were used and p values ≤ 0.05 were considered significant.

A.3 Results

Thirty-five striped skunks (7 M, 28 F) were radio-tracked during 1,873 h (858 and 1,015 h of tracking for 1993 and 1994, respectively), yielding 3,821 locations of active skunks. During tracking, human disturbances preceded 4.3% of all locations.

Visual observations of skunks were predominant in early spring, and decreased in favour of auditive and short-range triangulation locations with vegetative growth in summer (Fig. A1). Most locations (87%, $n = 3,647$) were performed at distances >10 m from radio-tracked skunks,

whereas 68% and 46% of the locations were at distances >15 and >20 m from skunks, respectively (Fig. A2).

I did not detect an effect of human disturbance on movement between consecutive 15-min locations (Wilcoxon signed-rank test, $T_+ = 136$, $Z = -0.4$, $P = 0.70$). Similarly, distance moved between consecutive 15-min locations was not influenced by distance from observer (Friedman two-way analysis of variance, $F_r = 6.6$, $n = 19$, $k = 4$, $P = 0.09$), although skunks moved slightly longer distances when observations were taken <5 m away (Fig. A3).

Observation type was autocorrelated with cover height ($\chi^2 = 466.8$, $df = 4$, $P < 0.01$), and disturbance was more likely to occur in shorter vegetation ($\chi^2 = 22.8$, $df = 2$, $P < 0.01$), and following visual observations ($\chi^2 = 19.1$, $df = 2$, $P < 0.01$). I analyzed changes in cover height only for skunks located in vegetation height class two to prevent a systematic bias associated with cover height category 1 (0-0.5 m) and 3 (>1 m) (e.g., skunk in height class one can only change to taller cover and vice versa for height class three). Skunks changed vegetation height classes independently of observation type ($\chi^2 = 1.13$, $df = 2$, $P = 0.57$), or disturbance (Fisher's exact test, $P = 0.21$). Similarly, skunks did not change habitats more often following human disturbance ($\chi^2 = 2.07$, $df = 1$, $P = 0.15$), or whether the previous observation was visual, auditive, or triangulation ($\chi^2 = 4.03$, $df = 2$, $P = 0.13$). When

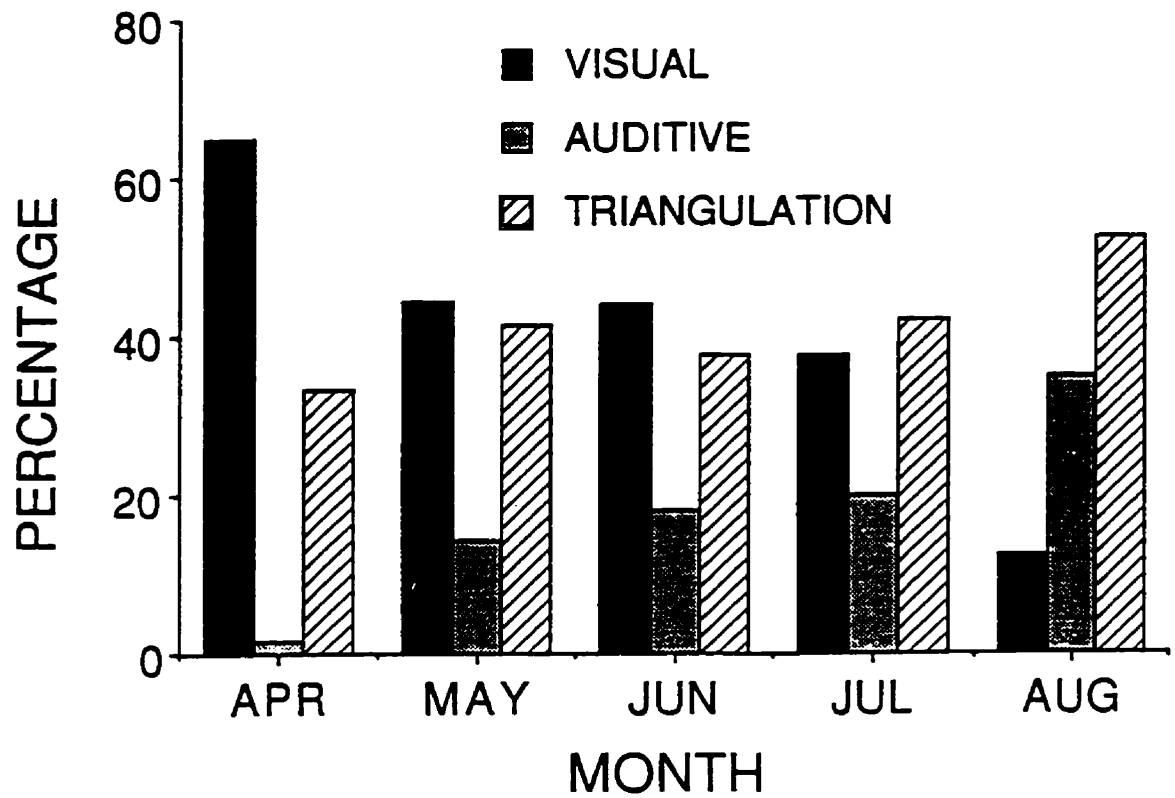


Figure A1. Type of observations used for locating radio-collared striped skunks at night during April through August, 1993-1994, in southcentral Saskatchewan ($n = 3,647$ locations).

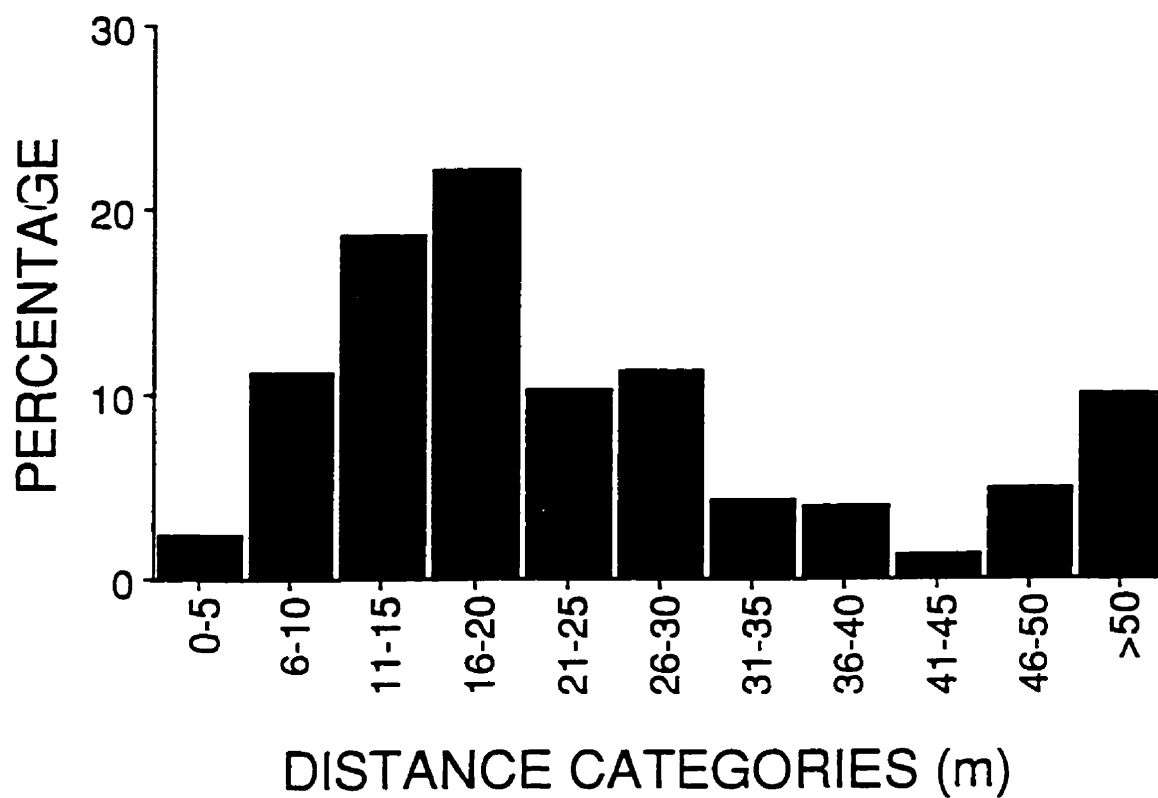


Figure A2. Distances between observers and striped skunks during each location during April through August, 1993-1994, in southcentral Saskatchewan ($n = 3,647$ locations).

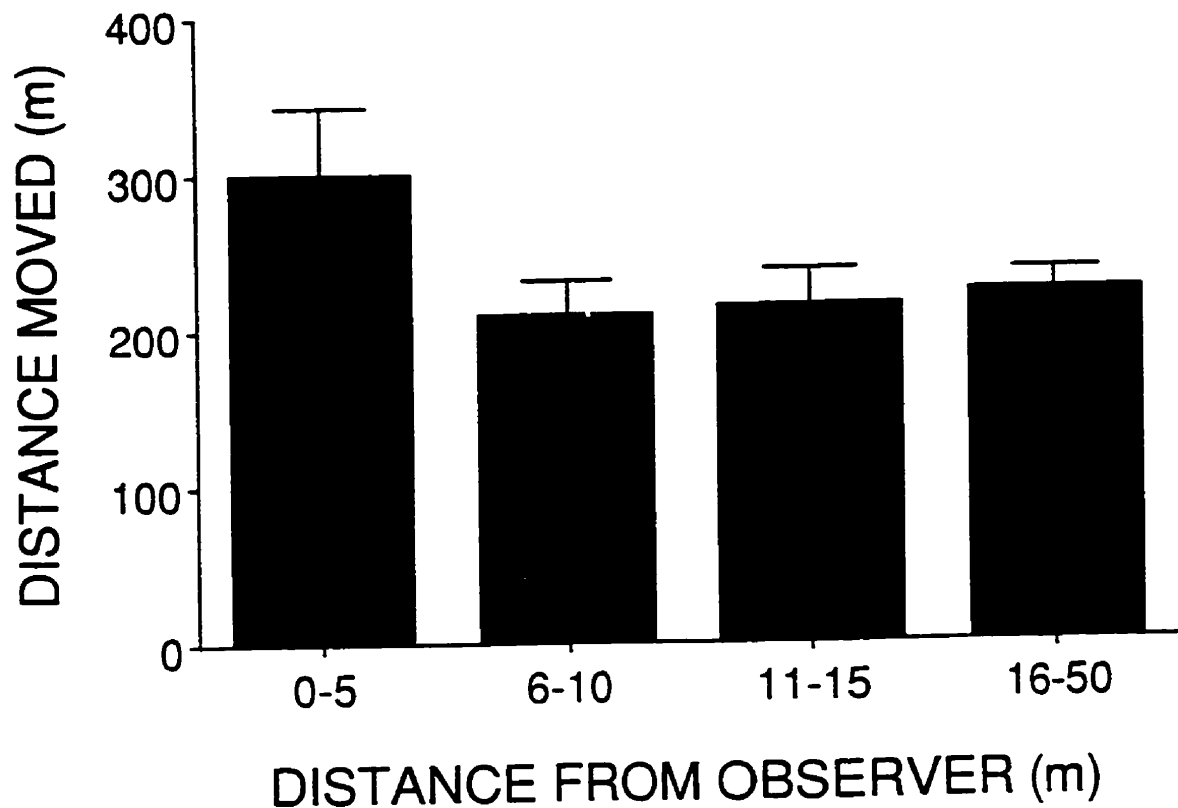


Figure A3. Distance moved between consecutive 15-min locations in relation to distance between observer and striped skunks during April through August, 1993-1994, in southcentral Saskatchewan ($n = 19$ striped skunks).

habitats were classified upon their density and cover thickness, skunks did not show any tendencies to go for denser or sparser habitat types depending on the observation type ($\chi^2 = 3.73$, $df = 2$, $P = 0.16$). However, disturbed skunks remained in the same cover type more than undisturbed skunks (Fisher's exact test, $P = 0.03$).

A.4 Discussion

Although my design lacked a true control level (i.e., observer present versus observer not present), the lack of effect of disturbance and observer distance on movement and habitat use suggests that the presence of an observer had minimal influence on the behaviour and space-use patterns of free-ranging striped skunks. Striped skunks rely on aposematic behaviour to deter predators (Larivière and Messier 1996c; Walton and Larivière 1994), and aposematic behaviour is effective and displayed only when predators are in close proximity (Larivière and Messier 1996c; Walton and Larivière 1994; see also Cott 1940; Cloudsley-Thompson 1980). This may explain why skunks are so tolerant of human observers. Furthermore, skunks commonly display short (<2 min) defensive behaviours during nightly foraging expeditions, often to non-predatory species (Larivière and Messier 1996c). Finally, striped skunks are nearsighted, and rely more strongly on olfaction and audition to locate prey and predators (Langley 1979; Larivière and Messier

1996c; Nams 1991). By remaining silent and downwind, observers could successfully observe foraging animals and rarely (< 5% of locations) induced defensive reactions. Furthermore, direct observation enabled radio-trackers to observe interactions between skunks and predators, prey, or other species (Larivière and Messier 1996c; Larivière and Messier 1997; Walton and Larivière 1994).

Use of cover as an escape strategy by striped skunks is unusual (Larivière and Messier 1996c). Data presented above showed that skunks do not change cover type (based on cover height or habitat type) following disturbance, or whether located by sight, sound, or triangulation. However, disturbed skunks tended to remain in the same cover type. For this reason, and to prevent any possible bias arising from unnoticeable disturbance events or observer-related stress, I recommend that locations immediately following a disturbance event should be excluded from behavioural analyses. Nonetheless, I believe that close-range radio-tracking is a better technique than conventional triangulation methods, especially when studying relatively slow moving mammals that use close-range defense mechanisms (i.e. striped skunks, porcupines, Erethizon dorsatum) and fine-grained habitats such as fragmented farmland/prairie landscapes.

A.5 Literature cited

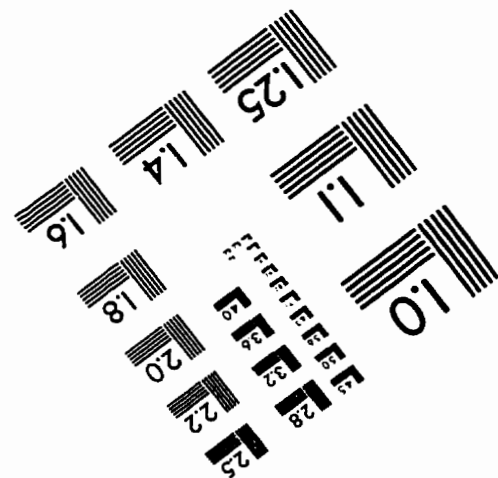
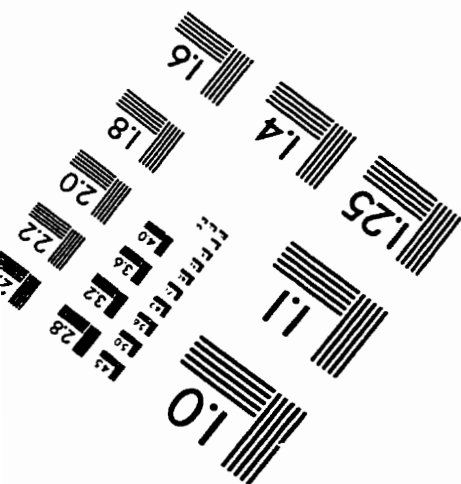
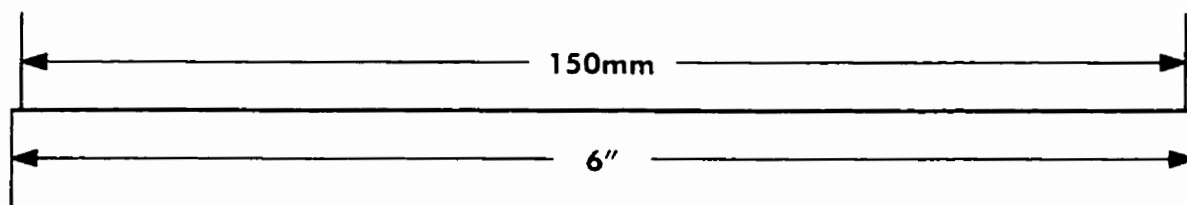
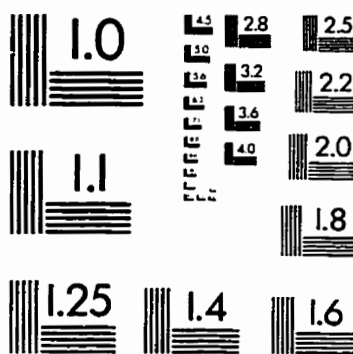
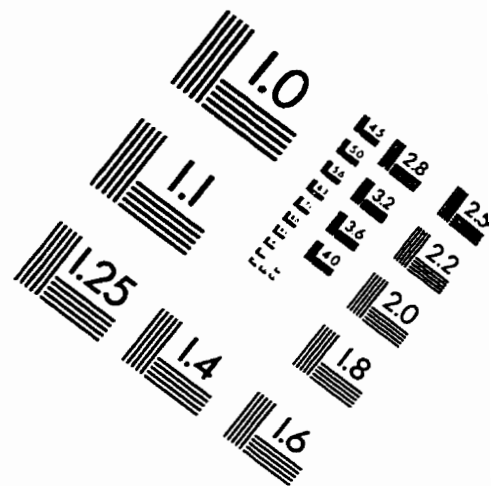
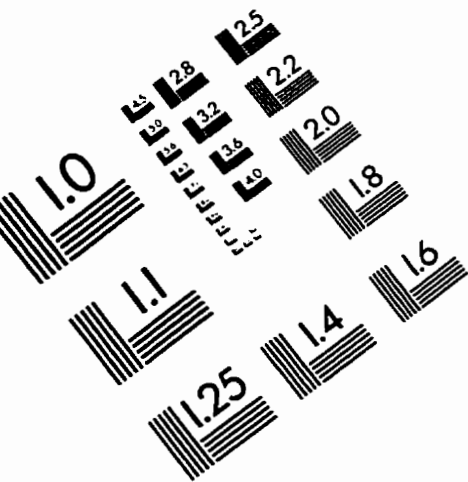
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IMAGE EVALUATION TEST TARGET (QA-3)



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